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UPPER CAMBRIAN FAUNAS FROM THE NORTHWEST WIND RIVER MOUNTAINS, WYOMING. PART I

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ABSTRACT—Dresbachian and early Franconian faunas from two measured sections near Green River Lakes in the northwestern Wind River Mountains, Wyoming are described in several papers. Part I gives the stratigraphy of the sections and describes and discusses the assemblages from the *Conaspis*, *Elvinia*, *Aphelaspis* and *Crepicephalus* zones, the agnostids and brachiopods from the *Cedaria* zone and several trilobites of Middle Cambrian age. The larger trilobite assemblages of the *Cedaria* zone will be described in subsequent papers.

Faunules from the *Conaspis* zone contain five genera and species of brachiopods and four of trilobites. Within the *Eoorthis* subzone *Eoorthis* beds are developed locally, the first reported occurrence of this feature in the Cordilleran region. The base of the *Billingsella* subzone is also present, but all higher Cambrian strata have been eroded. A characteristic *Camaraspis* subzone faunule of ten genera and species of trilobites and two of brachiopods represent the *Elvinia* zone. The species of the Franconian faunas are all previously described forms from either the central Interior or the Cordilleran region.

The Open Door formation and the underlying DuNoir limestone are separated by a prominent disconformity which spans at least all of *Dunderbergia* zone time and early *Elvinia* zone time, when the area was emergent and undergoing erosion. In the Clear Creek section most of the *Aphelaspis* zone strata were removed. In the Sheep Mountain section 175 feet or more of strata, comprising the entire *Aphelaspis* and *Crepicephalus* zones and the upper third of the *Cedaria* zone, are missing.

The *Aphelaspis* faunule is known from two trilobite genera and species and the gastropod, *Hypseloconus*, collected from the top DuNoir bed in the Clear Creek section. Two faunules represent the *Crepicephalus* zone. A small faunule obtained a few inches below the *Aphelaspis* assemblage contains three genera and species of trilobites and one brachiopod. A larger faunule at the base of the zone contains one gastropod, three brachiopod and six trilobite species, including *Minicephalus primus*, a new genus and species. The form may be the ancestral stock of the Lecanopygidae.

The *Cedaria* zone assemblage contains calcareous algae, five genera and species of brachiopods, two genera and species of gastropods?, *Semicircularea* and *Hyolithes*, two different and stratigraphically significant forms of Eocrinoidea, a new species of Conchostracean, *Dielymella? trituberculata*, and 27 genera and at least 54 species of trilobites. Two species of agnostid, one new—*Baltagnostus wyomingensis*, and the proparian, *Holcacephalus tenerus*, are described. *H. tenerus* ranges through 95 feet of section and is considered a stable species indigenous to the Utah-Wyoming area.

Two small collections of late Middle Cambrian fossils are included. They represent two different horizons within the uppermost unnamed Middle Cambrian faunal zone. The highest faunule contains two trilobite genera and is referred to as the *Olenoides* subzone. The lower faunule contains three trilobite genera, including one new species and two new genera—*Josina festiva* in the Menomoniidae and *Americare tetonensis* (Resser) in the Anomocaridae. Additional material of *Ithyektyphus tetonensis* (Miller) suggests a close relation with *Modocia*. The horizon is referred to as the *Americare* subzone.

[1] Cost of one plate borne by senior author.

INTRODUCTION

FROM 1938 to 1941 the Geology Department of Texas Christian University had a field camp at Green River Lakes in the northwestern Wind River Mountains, Sublette County, Wyoming. Cambrian rocks crop out at a number of localities in the vicinity of the lakes and an undisturbed section is well exposed on the southeastern flank of Sheep Mountain. In 1940 the senior author visited the area at the invitation of Drs. F. E. Turner and G. M. Richmond. Collections were made through the entire Middle and Upper Cambrian sequence in the measured section on Sheep Mountain, and additional collections were obtained from a partially exposed section on the northwest side of Clear Creek. C. L. Baker (1946) published a geologic map of this area and a discussion of the regional geology. G. M. Richmond (1945) gave a composite measured section and descriptions of the formations for the northwest Wind River Mountains.

This paper described the Franconian and some of the Dresbachian fossil material which was collected by the senior author and the Texas Christian University students and staff. The junior author completed the preparation, preliminary identification and photography of the specimens. In 1955 the senior author submitted nearly all of the Middle Cambrian material in her possession to Dr. W. J. Morris of Occidental College, Los Angeles, for description and study. One small collection which was missed is included in this paper.

ACKNOWLEDGMENTS

The authors wish especially to thank Drs. C. L. Baker, F. E. Turner and G. M. Richmond for the invitation to the senior author to visit the area, their continued cooperation during the field work, and for furnishing previously collected material and information about the sections. The completion of the study was made possible by a Research Assistantship Grant to the junior author from the New Mexico Institute of Mining and Technology.

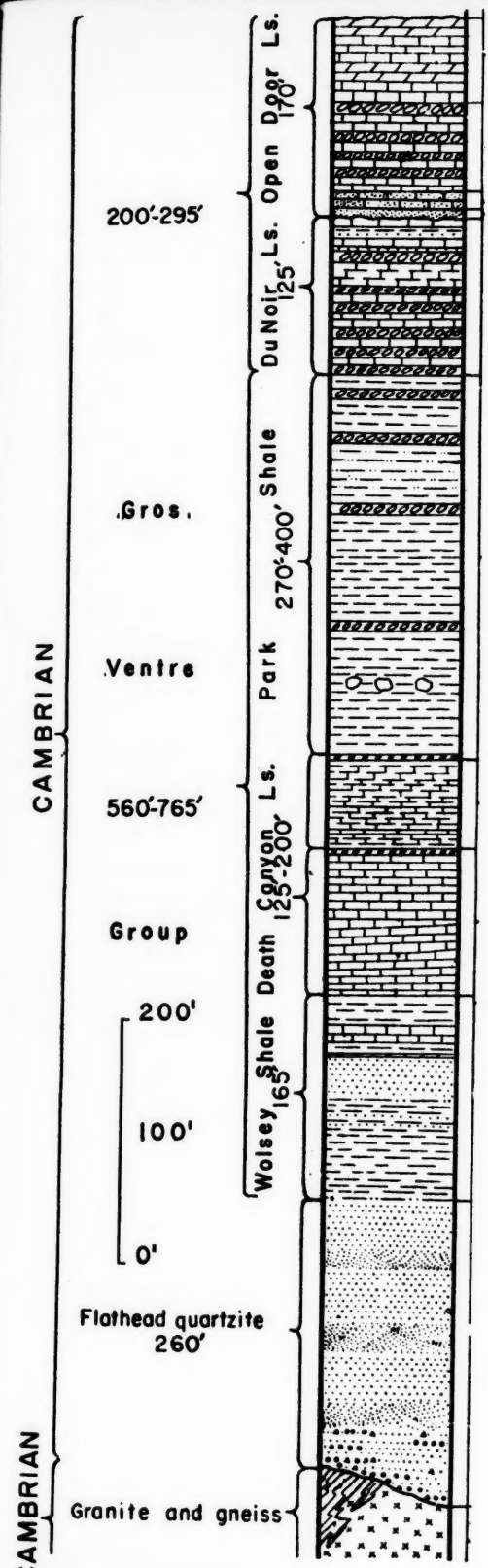
THE CAMBRIAN SECTION

A composite section for northeastern Sublette County, based largely upon the measured section on Sheep Mountain, was published by G. M. Richmond (1945). The lithic sequence is reproduced in text-figure 1 with the recent names of the lithic units as proposed by Shaw (1954), Shaw and DeLand (1955), and Lochman-Balk (1956).

The Flathead quartzite is the basal unit, the littoral sand deposits of the transgressing Middle Cambrian sea. Its medium to fine-grained, horizontal and cross-bedded sandstones grade near the top into the overlying shales. Linguloid brachiopods are occasionally found in these upper shaly sands but otherwise the unit is devoid of fossils.

Originally all the overlying Middle Cambrian lithic units were included in the Gros Ventre formation of Blackwelder (1918). In 1954 Shaw raised the Gros Ventre to group status and recognized three lithic units within it. The lowest unit is the Wolsey shale, a gray-brown to green-gray chloritic and micaceous shale with fucoid markings conspicuous on many of the irregular bedding planes. There is always a sandy shale transition zone at the base and locally, as at Sheep Mountain, a gray-brown, medium-grained glauconitic sandstone, 20 to 37 feet thick, may form a low cliff in the upper third of the unit. The sandstone is overlain by approximately 40 to 100 feet of olive-drab, thin-bedded micaceous shales intercalated with gray green to dirty brown lenses and thin beds of glauconitic or micaceous limestone. Trilobites may be found in both shales and limestones.

The Death Canyon limestone (Miller, 1936a) may contain from zero to as many as five shale units interbedded with the limestones depending upon the geographic location and individual interpretation of the section. Baker (1946, p. 570) places the base of the overlying Death Canyon at the base of a 15 foot cliff of dark gray to black dense medium-bedded limestone and includes an overlying 50 foot shale unit just below the main 115 foot limestone cliff. Richmond (1945) places the base of the formation at the base of this main cliff. This unit consists of blue-gray, thin-bedded, dense dolomitic limestone with thin gray silty and shaly partings. Small algal masses are scattered through the lower beds but trilobites could be collected only from the thin-bedded, gray crystalline limestone 15 to 20 feet from the



top. The cliff is overlain by 90 feet of gray, thin-bedded, fine-grained platy limestone or coarsely crystalline glauconitic limestone interbedded with gray green shales. An edgewise pebble conglomerate bed occurs at the base and another at the top of this shaley unit. The unit is included by Richmond in the Death Canyon limestone, but the amount of clastics is quite variable, and some workers have included it in the Park shale (Shaw, 1957).

The upper shale unit was called the Park shale by Shaw (1954). It is the lithic and stratigraphic equivalent of the Park shale of Montana. In this region the unit varies from 270 to 400 feet and the variation must be attributed to the arbitrary nature of the boundary both at the top and the bottom of the formation. In the Sheep Mountain section the shale is approximately 300 feet thick and forms a long partially covered slope of intercalated gray-green shales, thin beds of gray-green crystalline glauconitic limestone and thicker lenses of edgewise pebble conglomerates with a bioclastic limestone matrix. 60 to 70 feet above the base occur one or two horizons of *Tetonophycus*. Trilobites of two late Middle Cambrian subzones were collected in this unit, but no fossils of the highest—the *Bolaspidella*—subzone were found. A paraconformity may be present within the upper Park shales in this area.

The boundary between the Middle and Upper Cambrian falls within a series of interbedded shales and limestone pebble conglomerates which are usually placed in the top of the Park shale (DeLand and Shaw, 1956). Although the decided increase in the amount of limestone pebble conglomerates which occurs in the basal Dresbachian part of the section can be observed on the outcrop, most field workers prefer to draw the lithic boundary at the base of the DuNoir limestone cliff.

The DuNoir is a 125 foot cliff-forming unit of gray, coarsely crystalline, occasionally oolitic, mottled limestones, thin-bedded dense argillaceous limestones and flat or edgewise limestone pebble conglomerates

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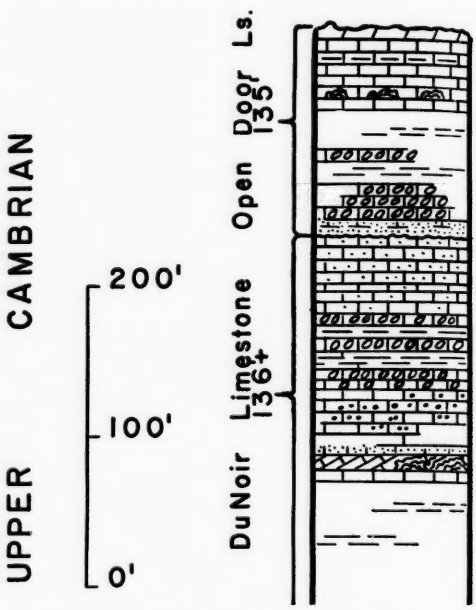
TEXT-FIG. *1*—The Sheep Mountain section.

intercalated with thin shale partings. A rough three-fold division may be observed—a lower unit in which the pebble conglomerates predominate, a middle unit predominately of oolitic mottled crystalline limestone, and an upper unit of both lithologies with several beds of fine-grained sandstones. In the Sheep Mountain section only *Cedaria* zone faunas were collected throughout the unit. In the poorly exposed Clear Creek section the upper third of the DuNoir is more complete, and fossils of the *Crepicephalus* and *Aphelaspis* zones were also obtained.

In both sections the top of the DuNoir is a conspicuous erosion surface marked by a sudden change in lithology. It is overlain abruptly by a 25 foot unit of buff-pink, fine to medium-grained, cross-bedded dolomitic sandstone grading upward into pink sandy mottled oolitic dolomitic limestone. This clastic unit is the lithic and stratigraphic equivalent of the Dry Creek shale of Montana as noted by Shaw (1954). No fossils were obtained from these beds.

The overlying Upper Cambrian beds comprise an interbedded shale and limestone unit varying in thickness from 150 feet to less than 70 feet, depending upon the amount of pre-Bighorn erosion. In the lower 25 to 50 feet edgewise limestone pebble conglomerates, thin shaly limestone and gray-green calcareous shales are interbedded. Mud cracks and ripple marks are common on the bedding planes. Trilobites of the *Elvinia* zone were obtained. A middle unit 25 to 30 feet thick consists of thin-bedded gray, medium-grained limestones in the upper 5 feet of which *Eoorthis* shells are abundant. The upper unit, when present, is a dove-gray, fine-grained limestone intercalated with lenses and thin beds of a coarse grained bioclastic limestone. It carries fossils of the *Conaspis* zone. The upper beds in any one section become increasingly more dolomitic and the brachiopod shells silicified toward the top. This highest Upper Cambrian unit is the lithic and stratigraphic equivalent of the Sage pebble conglomerate of southwestern Montana (Lochman-Balk, 1956). With the Dry Creek member at the base it was named the Open Door formation by DeLand (Shaw and DeLand, 1955).

On the north side of Clear Creek approximately 3 miles NE of Sheep Mountain a partial Upper Cambrian sequence is poorly exposed (figure 2). Structural relations in the region suggest that the two sections were originally deposited at sites much farther removed than their present positions. The Clear Creek section differs from that on Sheep Mountain in the occurrence of reef-like masses at several horizons. In the limestones of the *Conaspis* zone *Cryptozoon*-like masses were noted about 15 feet below the base of the Bighorn. In the DuNoir limestone a 2 foot algal reef of dense nodular limestone was noted at one locality just below a resistant limy sandstone ledge. About 200 yards to the southwest this same sandstone crops out along the lake shore. At this locality it is underlain by coarsely crystalline bioclastic limestone with an abundance of fossils. The faunas from this horizon indicate that the sandstone in the Clear Creek section is at the same stratigraphic position as the shaly sands near the top of the DuNoir in the Sheep Mountain section.



TEXT-FIG. 2—The Clear Creek section.

DISCUSSION OF THE FAUNAS

Description of Fossil Horizons and Faunal Lists

The megascopic lithologies and any significant insoluble residues are tabulated below for most of the collections. The horizons

are arranged in descending stratigraphic order for each of the sections.

The fossil horizons are indicated by a combination of letters and numbers for the senior author's collections, and by a combination of numbers alone for the collections made by Gordon Gulmon in 1939. Several collections made by F. E. Turner are so indicated. The types and figured specimens are deposited at the United States National Museum. Some species of brachiopods are figured with their associated trilobite faunas, but most of the brachiopod material has been given to Dr. W. C. Bell for study. Duplicate material is at the New Mexico Institute of Mining and Technology.

THE *CONASPIS* ZONE FAUNA

All published records of the *Conaspis* zone are from northwestern Wyoming sections, and even in those localities the assemblages are poorly represented. The authors' collections indicate that both incomplete collecting of the horizon and the subsequent pre-Bighorn erosion and/or dolomitization of the beds are responsible for the apparent paucity of species. *Taenicephalus* was the only previously recognized trilobite genus. Species of *Kendallina* and *Parabolinoides* are described in this paper. The presence and vertical range of the zone are primarily determined in these sections by the brachiopods, *Eoorthis* and *Billingsella*. The brachiopod assemblages are also prominent in the Yellowstone National Park sections (Bell, 1941). The northwestern Wyoming region differs noticeably from other areas of Wyoming and Montana in the separate development of the *Eoorthis* subzone as well as an overlying *Billingsella* subzone, and is thus comparable to the succession in the upper Mississippi Valley.

In the Clear Creek section the *Eoorthis* zone (horizon OC5) is represented by two lithofacies. 1) a gray calcilutite filled with large unbroken *Eoorthis* valves, some fewer, smaller valves of *Otusia* and *Ocnerorthis* and separate crinoid stems. This facies occurs as lenses 1 foot or less thick and is considered an insitu coquinite of the *Eoorthis* meadows. 2) a medium-grained bioclastic limestone of numerous crinoid stem joints, many slightly broken *Eoorthis* valves, a few valves of *Ocnerorthis* and *Billingsella*, and numerous oolites. This facies is interpreted as the wave-sorted debris accumulated along the margins of the *Eoorthis* meadows. Both facies appear to represent an environment of shallow, well-oxygenated water. Trilobite remains are essentially absent from the collections from both lithofacies.

The *Billingsella* zone (horizon OC6) is recognizable 5 feet above OC5 and continues through the overlying beds. It is characterized by an abundance of small, light-weight *Billingsella* valves, a moderate number of trilobite remains, numerous oolites and the absence of any valves of *Otusia*, *Ocnerorthis* and *Eoorthis*. The trilobite remains are broken and the material is clearly a current or wave-carried debris deposit. The larger number of trilobite remains with *Billingsella* is interpreted as indicating that the organisms were derived from moderate water depths.

It is believed that ecologic conditions as well as a time factor determined the development of the two brachiopod subzones in any one region. The presence of clear water, surf-washed shoals during the early part of *Conaspis* zone time was the prerequisite for the development of the *Eoorthis* meadows. Through eastern and central Montana and all of Wyoming except the northwestern area, the sea floor appears to have been shallow enough but the opacity of the water was high and wave or current action apparently relatively weak. Bell (1941) lists brachiopod faunas of the *Eoorthis* sub-zone from thirteen localities in southwestern Montana, from Yogo Gulch on the north into Yellowstone National Park on the south. All of these localities are as far or farther west than the Sheep Mountain section. The distance from the known Franconian shoreline would explain the lessened opacity, and the presence of a broad submarine ridge extending north-south on the Cambrian sea floor would provide the necessary surf-washed shoal conditions. The geographic position of the *Eoorthis* meadows of the *Conaspis* zone coincides with the sites of the *Collenia magna* reefs of the *Elvinia* zone and lends strong support to the thesis of the existence of a submarine ridge across the region during the early Franconian.

The association of brachiopod genera is similar throughout the region. *Eoorthis remnicha* occurs alone or with *Otusia sand-*

(*Text continued on page 800*)

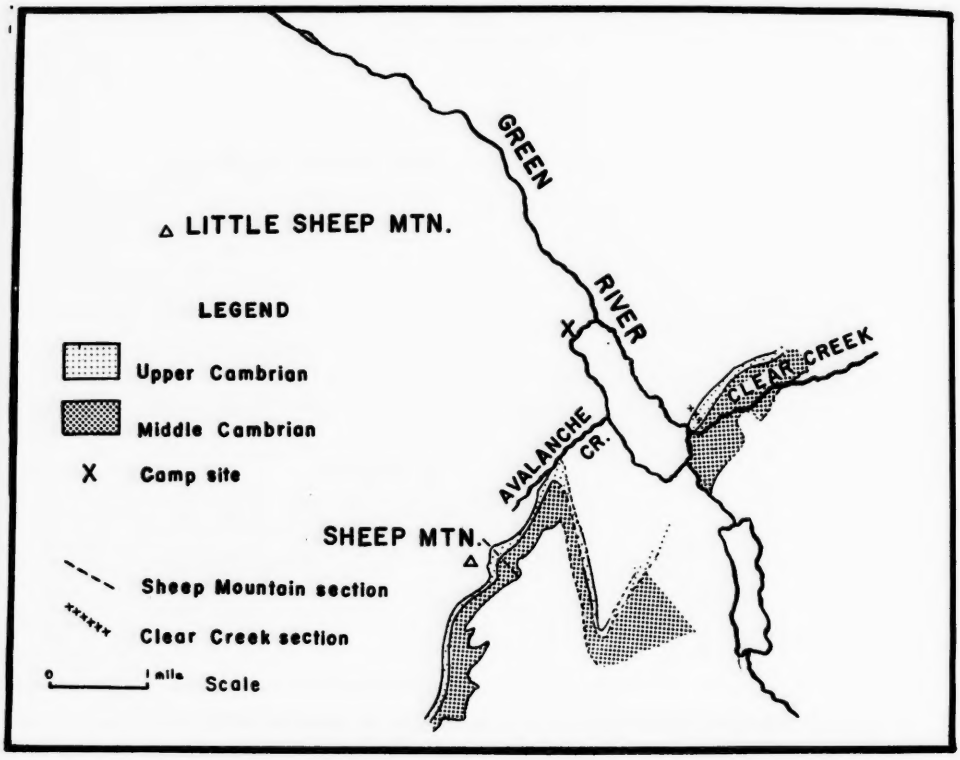
Clear Creek Section

OC9—1 to 3 inches below base of Bighorn dolomite Fine grained, dove-gray, sugary dolomitic limestone with silicified brachiopods *Billingsella* sp.	
OC8—1 foot below base of Bighorn dolomite Fine grained, gray, sugary dolomitic limestone, brachiopods silicified *Billingsella* sp. *Taenicephalus* sp. undet.	
OC7—10 feet below base of Bighorn dolomite Fine grained, gray, bioclastic limestone *Billingsella* sp. *Taenicephalus* sp. undet.	
OC6—(Turner—NE-47) 12 to 13 feet below base of Bighorn dolomite Fine grained, gray, glauconitic bioclastic limestone: residues contain a few large pitted quartz sand grains, some fine quartz sand, mica flakes and small clusters of limonite pseudomorphs after pyrite *Billingsella* sp. *Lingulella* sp. *Pseudagnostus* cf. *P. prolongus* (Whitfield) *Taenicephalus shumardi* (Hall) *Kendallina eryon* (Hall)	*Conaspis* Zone
OC5—18 to 20 feet below base of Bighorn dolomite=OC10 (Gulmon) at 10,300′ elevation northeast above Clear Creek Two lithologies—1) blue-gray, medium-grained *Eoorthis* coquinite; 2) pale-gray, coarse-grained bioclastic limestone: residues contain numerous large frosted quartz sand grains, large rounded glauconite grains, and clusters of limonite pseudomorphs Crinoid and/or Cystoid stems Problematica I *Eoorthis remnicha* (Winchell) *Parabolinoides* cf. *P. expansus* Nelson *Otusia sandbergi* (Winchell) cf. *Ocnerorthis cooperi* Bell	
N1—22 to 24 feet above base of Dry Creek sandstone member Mottled brown to gray, oolitic sandy limestone: residues contain oolites of dolomite rhombs, some large to medium glauconite grains, masses of spongy white silica, a few limonite pseudomorphs of pyrite *Pterocephalia bridgei* Resser *Camaraspis convexa* (Whitfield) *Deckera* cf. *D. completa* Wilson *Cliffia lataegenae* (Wilson) *Burnetia* cf. *B. alta* Resser *Dellea suada* (Walcott) *Linnarssonella girtyi* (Walcott) *Ocnerorthis cooperi* Bell *Elvinia roemeri* (Shumard)	*Elvinia* Zone-*Camaraspis* subzone
OC1a—½ to 1 foot below top of DuNoir limestone Thin-bedded, dense to fine-grained, dark gray-brown limestone mottled with light brown, coarsely crystalline areas *Glaphyraspis occidentalis* Lochman *Cheilocephalus* sp. undet. *Hypseloconus simplex* Lochman	*Aphelaspis* Zone
OC1b—1–2 feet below top of DuNoir limestone Medium-grained, pale buff-gray, glauconitic sandy mottled bioclastic limestone; medium-sized frosted quartz grains sparsely scattered through limestone and locally concentrated in thin stringers, brown calcite grains and pellets also abundant. *Tricrepicephalus* sp. undet. *Uncaspis* sp. undet. *Coosina ariston* (Walcott) *Dicellomus* sp. undet.	
OC2—37 to 40 feet below top of DuNoir limestone Coarse limestone pebble conglomerate with pale gray bioclastic crystalline limestone matrix: pebble of dense, gray limestone, often coated with glauconite; residues contain a few coarse quartz sand grains, many masses of limonite pseudomorphs of pyrite *Minicephalus primus*, n. gen., n. sp.	*Crepicephalus* Zone

Tricrepicephalus cf. *coria* (Walcott)	
Lonchocephalus sp. undet.	
Maryvillia sp. undet.	Base of *Crepicephalus* Zone
cf. *Coosina* sp. undet.	
Kormagnostus sp. undet.	
cf. *Billingsella* sp.	
cf. *Dictyonina* sp.	
cf. *Dicellomus* sp.	
Semicirculorea arcuata Lochman	
OC3—118–120 feet below top of DuNoir limestone	Base of upper *Cedaria* subzone
OC4—127 feet below top of DuNoir limestone = (Turner—40–34)	

Sheep Mountain Section

39-16—6 inches below base of Bighorn dolomite	
Pinkish-buff, dense, sugary dolomitic limestone	
Parabolinoides expansus Nelson	
Billingsella sp.	
39-11 and 39-12—38 feet below base of Bighorn dolomite	*Conaspis* Zone
Pale gray glauconitic medium-grained bioclastic limestone	
Parabolinoides expansus Nelson	
Billingsella perfecta Ulrich and Cooper	
Eoorthis remnicha (Winchell)	
39-4 and 39-5—75 feet below base of Bighorn dolomite	
Thin-bedded, gray-buff, coarsely crystalline bioclastic limestone interbedded with fissile green shales	
Cliffia lataegenae (Wilson)	
Camaraspis convexa (Whitfield)	
Burnetia cf. *B. alta* Resser	
38-5—80 feet below base of Bighorn dolomite	
Gray-green, platy coquinite with shaly calcilutite matrix, interbedded with gray-green calcareous shales	*Elvinia* Zone
Crinoid and/or Cystoid stems	
Ocnerorthis cooperi Bell	
Elvinia roemeri (Shumard)	
Dellea suada (Walcott)	
Housia sp. undet.	
Dokimocephalus sp. undet.	
Kyphocephalus sp. undet.	
Linnarssonella girtyi (Walcott)	
39-54—at top of DuNoir limestone	
39-50—1 foot below top of DuNoir limestone	Base of upper *Cedaria* subzone
SM1—5 feet below top of DuNoir limestone	
SM2—6.5 feet below top of DuNoir limestone	
SM2a—7.5 feet below top of DuNoir limestone	
SM3—65 feet below top of DuNoir limestone	
SM4—89 feet below top of DuNoir limestone	
SM5—92 feet below top of DuNoir limestone	
SM6—94.5 feet below top of DuNoir limestone	Middle *Cedaria* subzone
SM7—95.5 feet below top of DuNoir limestone	
SM8—97 feet below top of DuNoir limestone	
SM8a—97.5 feet below top of DuNoir limestone	
38-4—105 feet below top of DuNoir limestone	
39-51—117 feet below top of DuNoir limestone	Lower *Cedaria* subzone
SM10—120 feet below top of DuNoir limestone	
39-49—75 feet below base of DuNoir limestone	
Medium-sized limestone pebble conglomerate with light gray calcilutite matrix—a lens in gray-green micaceous shales	
Olenoides sp. undet.	
39-46—100 feet below base of DuNoir limestone	Middle Cambrian *Olenoides* subzone
Thin-bedded, gray-buff, medium grained glauconitic bioclastic limestone interbedded in gray-green calcareous shales	
Mcnairia inornata Deiss	
Olenoides cf. *O. incertus* Shaw	
SM21—25 to 35 feet above top of Death Canyon limestone	
Thin-bedded, dove-gray to buff, glauconitic coquinites intercalated with fissile gray-green micaceous shales	Middle Cambrian *Americare* subzone
Americare tetonensis (Resser)	
Ithyektyphus tetonensis (Miller)	
Josina festiva, n. gen., n. sp.	



TEXT-FIG. 3—Green River Lakes area showing location of sections.

bergi, a species of *Ocnerorthis* and one or more species of *Billingsella*. In the Sheep Mountain region the higher beds (horizon OC6 and higher), which are distinguished by the disappearance of all genera but *Billingsella*, are regarded as actually later in age than any *Eoorthis remnicha* faunas, as well as representing deposition in a different environment. The species of trilobites from OC6 occur in the middle part of the *Taenicephalus* subzone in Wisconsin (Berg, 1953). There probably was a significant hiatus in deposition in the Sheep Mountain region between horizons OC5 and OC6.

The one to five feet of beds carrying *Eoorthis remnicha* are directly correlatable with the *Eoorthis remnicha* subzone as it is developed in Wisconsin, Texas, southwestern Montana and northwestern Wyoming. Horizon OC6 and all higher beds preserved in this region are regarded as belonging to the *Billingsella* subzone. They are correlated with the *Taenicephalus* beds in Sweetwater Canyon, Wyoming (DeLand and Shaw, 1956), the *Taenicephalus-Billingsella* beds in the Horseshoe Hills, Montana (Grant, 1958) and the middle part of the *Taenicephalus* subzone of the upper Mississippi valley (Berg, 1953).

THE *ELVINIA* ZONE FAUNA

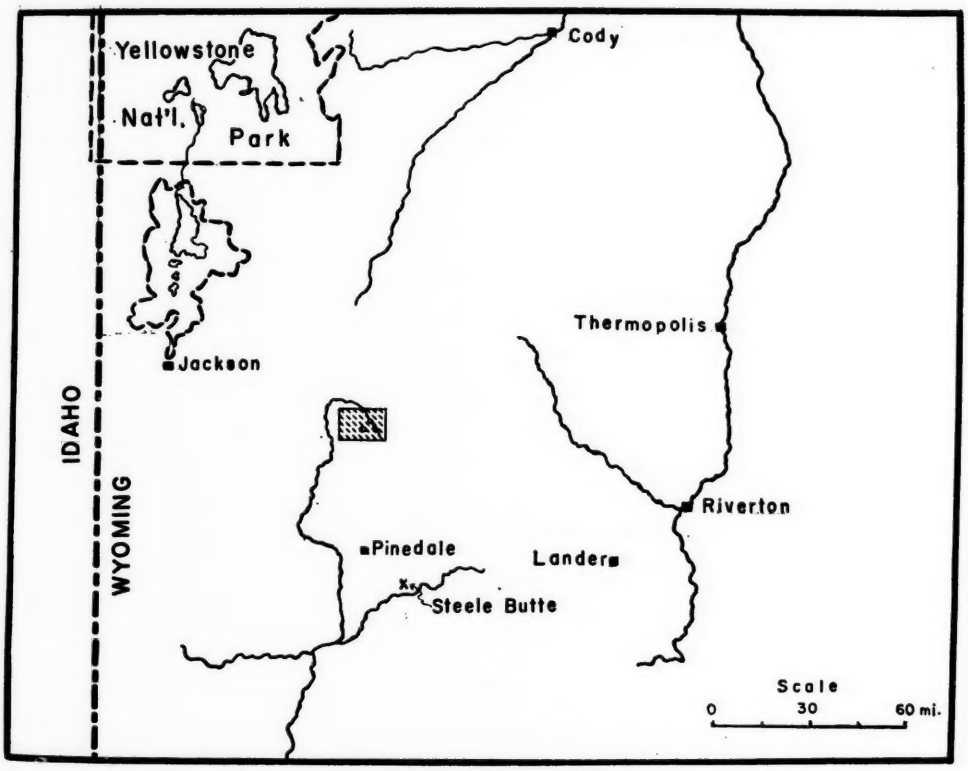
Numerous small collections from both sections suggest that faunas of this zone are well represented in the area, but the shale covered slopes of this part of the section have hindered adequate collecting. Most of the specimens are on the weathered surfaces of thin platy limestones intercalated with the shales. The best material (N1) comes from sandy limestones at the top of the Dry Creek sandstone member before the shale appears in the section. The poor preservation of the weathered specimens makes specific determination impossible in many cases.

The most common species are *Elvinia*

roemeri, *Dellea suada*, *Cliffia lataegenae* and *Camaraspis convexa*, all species of cosmopolitan occurrence in the cratonic faunas of North America. The peeled cranidia assigned to *C. convexa* show moderate convexity and distinct furrows and eye ridges. In this respect they are not as smooth or strongly convex as specimens from the upper Mississippi valley; but they certainly are not as flat as *C. plana* from Oklahoma. *Pterocephalia bridgei* and *Burnetia* cf. *B. alta* are species which were first described from the Davis formation of Missouri. The appearance of these two species in the *Elvinia* assemblages is especially significant when considered in connection with the similar relationship between the faunas of the two regions which is also present in the *Cedaria* zone assemblages. It affirms the reality of the existence of similar ecologic conditions between the two regions both at the two particular times indicated and probably during most of Upper Cambrian as well.

The single cranidium of *Deckera* appears more similar to that of *D. completa*, described by Wilson from the Ore Hill assemblage of Pennsylvania, than to that of the genotype, *D. aldenensis* Frederickson from Oklahoma; but the significance of this feature cannot be appreciated without more specimens. *Housia*, *Dokimocephalus* and *Kyphocephalus*, all common genera in the *Elvinia* assemblages, are represented by a few badly weathered cranidia and pygidia.

Two brachiopods are present, the ubiquitous *Linnarssonella girtyi* and the less common articulate, *Ocnerorthis cooperi*. The large numbers of the small well preserved valves of *Linnarssonella* scattered among the trilobite coquinas of these collections suggest that the species was indigenous to the sites of deposition. The scattered piles of trilobite molts afforded suitable sites of attachment on what was otherwise a soft bottom of calcareous ooze. The rarer shells of *Ocnerorthis* are part of the coquinal debris.



TEXT-FIG. 4—Index map of Wyoming.

Grant (1958) has obtained valves of *Ocnerorthis monticola* in association with an *Elvinia* fauna in Montana. The presence of *O. cooperi* in the *Elvinia* fauna and probably in the overlying *Eoorthis* subzone in this region suggests that the upper half of the *Elvinia* zone and the lower half of the *Conaspis* zone may constitute the biozone of the genus. The distinctive, easily recognized shell of *Ocnerorthis* would make the genus a valuable guide fossil in the Cordilleran region.

All the collections appear to contain assemblages of the upper half of the *Elvinia* zone which may be called the *Camaraspis* subzone. No specimens of *Irvingella* were found nor is there any indication of an *Irvingella major* subzone in these sections. There is no published record of the occurrence in Wyoming of the trilobite assemblage diagnostic of the *I. major* subzone, and only a few unpublished occurrences of *I. major* are known. The *Elvinia* assemblages described by DeLand and Shaw (1956) from Steele Butte, Sweetwater Canyon and Granite Falls all belong to the *Camaraspis* subzone and are directly correlatable with the assemblages from the Sheep Mountain region. However, all the collections are small and the sections throughout northwest Wyoming and southwest Montana have not been thoroughly examined and collected. It is not now possible to decide whether the absence of an *Irvingella major* epibole in these sections is to be attributed to the existence of unfavorable ecologic conditions across the entire region, or to an actual cessation of deposition toward the end of *Elvinia* zone time.

THE *APHELASPIS* ZONE FAUNA

One small collection (OC1a) obtained from near the top of the DuNoir limestone in the Clear Creek section is the only evidence of the *Aphelaspis* zone assemblage in this region. This material demonstrates that the area was still receiving deposition at least during the early part of *Aphelaspis* zone time. The prominent and widespread disconformity at the top of the DuNoir presumably must have occurred during *Dunderbergia* zone time.

Glaphyraspis occidentalis, *Hypseloconus simplex*, and *Cheilocephalus* are characteristic of the lower *Aphelaspis* subzone and are normal members of this assemblage wherever it is found in western Wyoming and southwestern Montana. The absence of *Aphelaspis* is attributed to the small size of the collection.

The specimens occur as fragments sparsely scattered through a light gray calcilutite. *Glaphyraspis* fragments are by far the most abundant, and the soft lime bottom may have been the habitat of this species. But *Hypseloconus* is believed to have been a near-shore dweller, and the few shells were washed into this area. In the material from Steele Butte specimens of *Hypseloconus* are larger and much more abundant. This site was much closer to the Upper Cambrian shoreline position than the Sheep Mountain region. The rapid increase in clastics which occurs in the Upper Cambrian beds in a south and southeast direction along the Wind River Mountains confirms the paleontologic conclusions.

The beds containing this small collection are directly correlatable with the lower half of the *Aphelaspis* zone. The horizon is also known at Steele Butte and Beartooth Butte in Wyoming and in the Logan, Nixon Gulch and Picket Pin Ridge sections of southwestern Montana.

THE *CREPICEPHALUS* ZONE FAUNA

Two small collections (horizons OC1b and OC2) lie within the *Crepicephalus* zone in the Clear Creek section. Their presence at this one locality suggests that deposition did occur throughout the area of the northwest Wind River Mountains during *Crepicephalus* zone time and that differential warping and erosion at the end of the Dresbachian were responsible for the removal of all the beds of this zone as well as those of the *Aphelaspis* zone from most of the area.

The specimens of OC1b occur as sparsely scattered, broken and now weathered fragments in a light gray mottled oolitic coarsely crystalline limestone. The few trilobite fragments have been carried some distance, apparently into a shallower water site than the normal habitat of the trilobites. Only three trilobite genera and the brachiopod *Dicellomus* were found. *Uncaspis* is represented by a typical adult pygidium. This genus

ranges through the *Crepicephalus* zone. *Coosina ariston* (Walcott) both in Montana and Texas is particularly diagnostic of the upper two-thirds of the *Crepicephalus* zone. *Tricrepicephalus* and *Dicellomus* range through most of the Dresbachian. Horizon OC1b is correlated with the upper half of the *Crepicephalus* zone. Beds of this age are known throughout south central and southwestern Montana and in Wyoming southward to the southern end of the Wind River Mountains and eastward throughout the Bighorn Mountains.

A larger fauna (horizon OC2) was obtained from the crystalline calcite matrix of a prominent limestone pebble conglomerate at the base of the upper mottled oolitic limestone, approximately 35 feet below horizon OC1b. The specimens appear to represent the disarticulated molts of several trilobites which were the normal habitants of the area.

The largest number of cranidia, pygidia, librigenae and thoracic segments are referred to *Tricrepicephalus coria*, a species first described by Walcott from several weathered cranidia from the House Range, Utah. Palmer (1954) placed seven species in synonymy with *T. coria;* but apparently topotype material was neither collected nor studied by Palmer at the time. The Wyoming cranidia have narrow, slit-like pits in the anterior border furrow similar to those on the cotype cranidia of *T. coria;* but the anterior border is moderately nasute—a feature which is not evident on the cotypes although it could have been destroyed or blurred by the weathering of the specimens. The Wyoming material is too small to give an idea of the amount and kind of intraspecific variation possible within this population. Until population studies of the species of *Tricrepicephalus* are made Palmer's extensive lumping of these species is suspect. The Wyoming specimens can only tentatively be referred to the Utah species.

Minicephalus primus, new genus, new species, is, with *T. coria*, the most abundant form in the assemblage. Additional collecting should be done to increase our knowledge of this interesting form. The 5 cranidia, 2 librigenae and 13 pygidia show a moderate size range. The structure of the known parts of the exoskeleton is very similar to the characteristic structure of the late Upper Cambrian genera, *Lecanopyge* and *Resseraspis*. The authors believe they are fully justified in placing *Minicephalus* in the Lecanopygidae, making it the earliest known and probable ancestral genus of that family. The distinctly punctate inner surface and finely reticulate outer surface of the exoskeleton of *Minicephalus* are also features which are essentially unknown among Dresbachian trilobites, but are not uncommon in genera of Trempealeauan age. *Minicephalus* is the first genus recorded from any of the Dresbachian cratonic assemblages which can be considered as a probable ancestor of one of the late Upper Cambrian trilobite families. It is possible that other ancestral genera of the *Prosaukia* and *Saukia* assemblages were indigenous to the western and northwestern Cordilleran regions during the Dresbachian.

Two small pygidia are identified as *Coosina*. Their worn and fragmentary condition prevents specific identification. The smaller pygidium has exactly the same shape as a small pygidium of *Coosina ariston* from OC1b but the outer surface is smooth—a feature which could have been caused by wear during transportation. Two other small pygidia are identified as *Maryvillia*. Both are peeled specimens and cannot be certainly referred to either *M. arion* Walcott, the genotype, or *M. eleanora* (Lochman), the Montana species of comparable age. The distinguishable features appear to place it between the two described species. It may represent either a new species or a distinct intraspecific variation of *M. eleanora*. A single pygidium is identified as *Lonchocephalus*, but a cranidium is needed for accurate specific determination. The triangular shape of the pygidium is most similar to that of *L. chippewaensis*, the genotype, from Wisconsin and quite unlike that of *L. montanensis* Lochman from Montana. Two species of *Lonchocephalus* based only on cranidia were described by Walcott from the House Range, Utah. It is quite possible that this pygidium may represent one of these species.

There are only a few associated non-trilobite species. Some shells of the small molluscan *Semicirculatarea arcuata* were obtained. The reduction in numbers of specimens, when compared to the lower horizons, suggest that this species is on the wane and

near the end of its life-span. Neither in these sections nor elsewhere in the adjoining Wyoming-Montana region has the species been recorded from any younger *Crepicephalus* zone assemblages. There are very few brachiopod specimens. Presumably the trilobite debris was derived largely from habitats unfavorable for brachiopods. A few shell fragments of *Dicellomus* and *Dictyonina* were noted. Several fragments of an articulate shell referred to *Billingsella* were found. It would appear that one or two genera of primitive Orthacea were becoming locally abundant in the *Crepicephalus* assemblages. Sporadic valves have been noted in these assemblages from Texas and Oklahoma as well as western Wyoming.

The fauna from OC2 is placed in the lower part of the *Crepicephalus* zone. The presence of *Lonchocephalus*, *T. coria* and *Coosina* and the absence of *Meteoraspis* are the diagnostic features in correlating the fauna. The small size of the assemblage is probably responsible for the absence of *Crepicephalus* and *Coosia*. This faunule is definitely somewhat younger than the basal *Crepicephalus* faunule from horizons 9.1 to 9.3 in the Half Moon Pass section. The Wyoming assemblage shows no *Cedaria* zone affinities among the trilobites whereas the Montana faunule is clearly a transitional assemblage between the *Cedaria* and *Crepicephalus* zones. Its equivalent may well be present in the covered portion of the Clear Creek section below horizon OC2.

CEDARIA ZONE FOSSILS

Most of the collections from the two sections belong to the *Cedaria* zone. A large number of trilobite species dominate these faunules. Inarticulate brachiopods are abundant in a few horizons and five genera and species were identified. The presumably planktonic mollusca, *Hyolithes primordialis* and *Semicirculatea arcuata*, are represented by specimens from nearly every horizon throughout the zone. Several other phyla are represented sporadically. Specimens of a calcareous algae are moderately abundant in three horizons, through about 35 feet of the Sheep Mountain section. Two different types of Eocrinoidea plates are recognized in the faunules from the Sheep Mountain section. The two types are segregated stratigraphically in this section, and show the same relationship as was observed in the southern Montana sections. A single valve referred questionably to the conchostracean genus *Dielymella* was obtained.

Among the trilobites two agnostid species were recognized—*Kormagnostus simplex* is moderately abundant and long ranging, but *Baltagnostus* is known from only a few specimens. The proparian *Holcacephalus tenerus* is described from a large number of specimens obtained from nearly every horizon in the Sheep Mountain section.

The few specimens of calcareous algae were obtained from the middle *Cedaria* subzone in the lower part of the DuNoir. The small (1–3 mm.) pear-shaped bodies are the same type as was described from the *Crepicephalus* zone in Montana and the upper *Cedaria* zone in Missouri. It is assumed that these algae were normal members of the *Cedaria-Crepicephalus* biota wherever a suitable habitat prevailed.

The brachiopods belong entirely to inarticulate genera and species with a long stratigraphic range (*Cedaria* through *Crepicephalus* zones) and a wide geographic range (Montana to Texas and Missouri). The Cordilleran and central United States brachiopod faunas comprise a single assemblage of western origins. More than 100 valves of *Dicellomus amblia* were obtained, over half of the material protegula from the insoluble residues. The abundance of protegula and small adults suggests that the spat settled on the debris of the trilobite molts. Valves of *Dysoristus lochmanae* are also abundant and suggest a similar habitat for this form; but the species appears to be limited to the upper part of the middle *Cedaria* subzone. This limited range also occurs in Montana and Missouri. *L. modesta*, a minor member of the middle *Cedaria* subzone, is also known from Missouri. The chitinophosphatic shell is small, fragile and usually broken. The specimens show some transportation indicating that *Lingulella* occupied a different habitat from that of *Dicellomus* and *Dysoristus*. *Micromitra modesta* is the most common Neotremata. The species ranges through the Sheep Mountain section but only a few valves were recovered from any one collection with the exception of SM7 in which protegula are abundant.

Many of the larger valves are broken at the hinge line suggesting that the specimens were torn from their place of attachment and washed into the debris piles. Among the specimens the same two types of surface ornamentation—1) only strong growth fila; or 2) growth fila crossed by radiating flexures—occurs as was observed on the Montana and Missouri valves. Rare broken specimens of *Dictyonina* appear limited to the top of the middle *Cedaria* subzone. The characteristic pitted surface ornamentation permits recognition of the genus. This form probably occupied the same habitat as *Micromitra modesta* but possessed a very brittle, fragile shell as most known specimens are fragmentary.

Hyolithes primordialis and *Semicircularea arcuata* range through the *Cedaria* zone and show marked similarities in their mode of occurrence. The moderate numbers of *H. primordialis* consist largely of broken, glauconitized or phosphatized internal molds which retain a trace of the shell. One small calcareophosphatic shell from the insoluble residue of SM8a has the minute details of the surface ornamentation well preserved but the specimen is very fragile. Adult shells reached a length of 60 mm., an aperture width of 20 mm. The shell was slightly curved. Two limestone molds of a flat circular object, about 6 mm. wide, covered with closely spaced concentric wrinkles, are interpreted as impressions of hyolithid opercula. The molds suggest that the original material was a tough semi-fiexible organic sheet. The predominance of internal molds indicates that these planktonic shells settled upon a sea floor where sedimentation was sporadic so that there was ample time for the molds to be glauconitized and decayed. The rare original shells happened to settle to the bottom just as the organic debris was being deposited. *Semicircularea arcuata* is a small slightly assymmetrically coiled shell classified as a gastropod. The form ranges through the *Cedaria* zone and into the base of the *Crepicephalus* zone, and reaches its maximum abundance at the top of the middle *Cedaria* subzone here as it did in Montana. The maximum shell size of 4 mm. is the largest noted for the genus. Most specimens are steinkerns but some are external molds showing the growth lines paralleling the oval aperture and crossed by diagonal costellae to form a spiral pattern. Many of the steinkerns are glauconitized or phosphatized like the hyolithid molds. This feature combined with the wide vertical and horizontal ranges of the species suggests that it, too, was a planktonic form.

The Agnostida are represented by abundant specimens of *Kormagnostus simplex* and a few specimens referred to a new species of *Baltagnostus*, which also occurs in the Steele Butte collections (DeLand and Shaw, 1956). Palmer (1954) recognized only the genotype, *B. centerensis*, and would restrict the genus to the late Middle Cambrian. However, an agnostid with a well defined anterior lobe on the cephalon and a narrow, nearly straight-sided axial lobe on the pygidium is a rare member of *Cedaria* assemblages in Montana and Wyoming. As these are Baltagnostid characteristics, it seems best to place the species in that genus rather than to consider it a very aberrant form of *Kormagnostus*. *Kormagnostus simplex*, represented by a moderate number of specimens, ranges through most of the *Cedaria* zone. The authors are accepting Palmer's diagnosis of *K. simplex* as a biospecies with a certain amount of variation, especially in the pygidium. The Wyoming specimens show several of the individual variations. In smaller pygidia (1 mm.) the sides of the pseudolobe tend to converge and the end does not reach the axial furrow. The terminal node of the axis can be distinguished on some specimens. On small pygidia it is right at the end of the pseudolobe but on larger specimens the inflation of the pseudolobe causes it to appear slightly anterior to the end. A common variation is in the course of the accessory furrow, from nearly straight to widely diverging and curved posteriorly. There is little or no variation in the cephalon other than the degree of faintness of the furrow around the anterior lobe of the glabella. *Kormagnostus* was a pseudoplanktonic form on floating sea weed. The molts and dead bodies settled down upon the sea floor and were incorporated into the debris piles. In SM6 there occurs a mixture of well preserved specimens and old pelletized specimens (of same dark brown, fine-grained calcite as associated pellets) which are worn and smooth like the calcite sand grains. This

association appears comparable to that noted for *Hyolithes*. A pseudoplanktonic life also best explains 1) the wide geographic distribution of the species and 2) the marked increase in abundance of specimens toward and in the geosynclinal sites. The biospecies of *Kormagnostus simplex* is recognized from southern Appalachians through central United States and the Cordilleran region to Montana. In the stable shelf sites sporadic specimens are known but their number is insignificant as compared to the abundance and variety of normal Opisthoparian species. In unstable shelf site collections (as the Wyoming material) *Kormagnostus* specimens are more numerous but still subordinate to the other trilobites of the assemblages. But in the Cordilleran and southern Appalachian geosynclinal sites the Agnostids become conspicuous as the normal benthonic species are reduced in numbers.

The abundance of adult and meraspid specimens of *Holcacephalus tenerus* and the long range, through 95 feet of section, are interpreted as indicating a species indigenous to the Utah-western Wyoming region. The species was first described from the House Range, Utah. Individual variations in the cranidium occur in the populations (see plate 4). The glabella varies in width and roundness of the anterior end. A median posterior inbending and obsolescence of the anterior border is another common variation which suggests a trend toward cranidia of the type of *H. tenerus cuneiferus* from Missouri. In SM2 some small cranidia show a pair of low nodes on the fixigenae opposite the base of the glabella, a feature also noted by Palmer (1954) on Texas cranidia 1.5 mm. in length. In the Wyoming material this feature occurs only on latest meraspid and early holaspid cranidia up to 1.5 mm. in length, but is not seen on larger cranidia.

LATE MIDDLE CAMBRIAN FOSSILS

Two small collections were missed when the Middle Cambrian material was sent to Dr. W. J. Morris. The several trilobites which they contain were studied and described.

From horizon 39–46, approximately 100 feet below the top of the Park shale, a single small cranidium referred to *Mcnairia inornata* Deiss and a fragmentary *Olenoides* cranidium was obtained. The monotypic *Mcnairia* was described from the late Middle Cambrian Steamboat limestone of northwestern Montana. The type is poorly preserved and the authors believe that a restudy of the genus with better material will probably demonstrate the synonymy of *Mcnairia* with *Parehmania*. In the authors' collections from the limestone pebble conglomerate ledges in the upper 150 feet of the Park shale slope large cranidia of *Olenoides* were conspicuous. This portion of the section may, for convenience, be called the *Olenoides* subzone. The fragmentary cranidium has been referred to *Olenoides incertus* Shaw in order to call attention to the latter species which was established upon the *Olenoides* pygidium obtained by Miller (1936b), from near the top of the Death Canyon limestone in Teton Creek Canyon. The correct identity of the Park cranidia must await a thorough study of the late Middle Cambrian faunas above the *Bathyuriscus-Elrathina* zone.

The second collection (SM21) came from thin bedded coquinal limestones intercalated with calcareous shales approximately 32 feet above the top of the Death Canyon limestone cliff. The 80 to 90 feet of section overlying the cliff form a steep slope rather than a cliff, and the unit has been placed both in the Death Canyon and the base of the Park shale. The thin platy limestones are frequently a coquina of cranidia and pygidia of *Americare*, previously referred to as *Glyphaspis* or *Glyphaspis*-like. Cranidia, pygidia, librigenae and hypostoma are now known for this species identified as *Americare tetonensis* (Resser), and the study of this material reveals that the form is related to but distinct from *Glyphaspis* to which Miller (1936b) and Resser (1937) had referred it. The pygidium, the only part previously described, is similar to that of *Glyphaspis* and appears to differ only in the greater definition of the narrow pleural furrows on the anterior segments. On the cranidium of *Americare* the anterior branch of the facial suture runs abruptly in toward the glabella leaving only a very narrow anterior edge of the palpebral area. This feature is common in the Eurasian genera of the Anomocaridae; but in *G. capella* (Walcott), the genotype, and other North American *Glyphaspis* species the anterior branch of the

facial suture makes a wider angle and the palpebral area is noticeably wider throughout. It is probable that *Americare* and *Glyphaspis* are related through their derivation from a common parent stock. The two genera may have biostratigraphic significance even though their biozones may partially overlap. *Glyphaspis* is characteristic of the top of the *Bathyuriscus-Elrathina* zone and may continue into the base of the overlying late Middle Cambrian unnamed faunal zone. *Americare* appears and is very abundant in the lower part of this unnamed zone, which is here referred to, for convenience, as the *Americare* subzone. *Americare* apparently ranges up into the middle portion of the unnamed zone; but there is no indication, as yet, that it occurs with members of the *Bolaspidella* subzone which lies at the top of the unnamed faunal zone.

Ithyektyphus was established by Shaw (1956b) for two species originally described by Miller from the northern Wind River Mountains and the Teton Range. In collection SM21 cranidia identified as *I. tetonensis* (Miller) are associated with pygidia and librigenae, thus considerably increasing our knowledge of this species. Numerous similarities between the cranidia and pygidia of *Ithyektyphus* and *Modocia* of the *Cedaria* zone suggest that the two genera are closely related and that *Ithyektyphus* is the immediate ancestor of *Modocia*. An examination should be made of specimens in the late Middle Cambrian faunas which have been referred to *Modocia*. *M. nevadensis* Palmer from the lower part of the Hamburg limestone, Eureka district, Nevada, is the only such species at present adequately illustrated and it appears to belong to *Ithyektyphus*. The type specimens of *I. tetonensis* (Miller) are cited by Miller as ranging through the upper 100 feet of his Death Canyon limestone member and are associated with *Americare tetonensis* Resser and *Bolaspidella resseri* (Miller). The horizon is believed to be approximately the same as that of the Sheep Mountain specimens, and the association is similar. A second valid species, *I. tipperaryensis* (Miller) was obtained by Miller in the Park shale 120 feet above the top of his Death Canyon. It has not been found in our small collections.

The third member of the faunule assemblage of SM21 is *Josina festiva*, new genus, new species. The cranidia of this small form place it as another member of the Menomoniidae and the possible common ancestor of several of the later Dresbachian genera of this family. In the elongate shape of the glabella the genus is decidedly different from all other members of the Menomoniidae. This feature is considered a valid generic character. Otherwise the cranidium of *Josina* possesses features which suggest affinities with both *Bolaspidella* and *Densonella*.

The assemblage of SM21 is placed in the lower part of the late Middle Cambrian unnamed fauna zone. The beds at this horizon may be placed by various authors either in the upper part of the Death Canyon limestone or in the lower half to third of the Park shale. The regressive nature of the entire upper half of the Middle Cambrian section throughout Wyoming prevents the subdivisions of the late Middle Cambrian unnamed faunal zone from being associated with particular and distinctive lithologies which might assist in recognition of the subzones. Only the fossils are presently reliable, and for the various faunules which appear to be present the probable ecologic variations have not yet been worked out.

PALEOGEOGRAPHIC RELATIONS

Western Wyoming and southwestern and central Montana were part of a single depositional area across which the faunas could move freely. The distribution pattern of the varied habitats controlled the presence and the relative abundance of the genera and species in each particular subregion. The central Montana shelf sites came under the influence of a major source of fine silt and clay from the northwest, a situation which increased the opacity of the water over the area and produced a preponderance of soft mud bottoms. Northern currents, reaching this area first, may also have produced a slightly lower overall temperature.

Southward the waters became clearer and clastic deposition fell off to a minimum along the Montana-Wyoming border. Shallow water depths were prevalent as much of the limestone is of pebble conglomerate origin; and algal growths are not uncommon. All the Montana sites are typical stable shelf areas occupied by characteristic stable shelf assemblages.

The western Wyoming sections from Beartooth Butte southward through the Western Wind River Mountains all show the influence of a northwest-southeast trending low positive axis projecting northward from the eastern Uinta Peninsula. As early as late Middle Cambrian time shoal areas along this axis furnished the sites for *Tetonophycus* meadows. During Dresbachian time this axis formed a submarine ridge with local shoals upon which algal reefs developed as at OC3. The ridge also apparently directed the silt laden currents northward from the Uinta Peninsula and was responsible for the sporadic but persistent appearance of clastics in sections clear to the Montana border. The southern origin of the clastics is demonstrated by their steady increase south and southeastward along the western Wind River Mountains until the entire section has become sandstone (the Lodore formation) in the Rawlins Hills and the eastern Uinta Mountains. Toward the end of the Dresbachian

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EXPLANATION OF PLATE 95

FIGS. *1–7—Cliffia lataegenae* (Wilson). *2*, small cranidium, ×6, U.S.N.M. 138222b; *4,5*, dorsal and profile of associated pygidium, ×11, U.S.N.M. 138222a, from 39–4. *1,3,7*, fragmentary cranidia, ×7, ×7, ×9, U.S.N.M. 138223b,a,c; *6*, associated librigena, ×7, U.S.N.M. 138223d, from N1.

8–11—Ocnerorthis cooperi Bell. *8,9*, exteriors of brachial valves, ×1.7, ×3.8, U.S.N.M. 138224a, c; *10*, interior of brachial valve, ×4, U.S.N.M. 138224b, all from N1. *11*, exterior of pedicle valve, ×4.8, U.S.N.M. 138225, from 39–16.

12–23,31—Taenicephalus shumardi (Hall). *12,13*, associated pygidia with 3 pairs of short marginal spines, ×5.4, ×6, U.S.N.M. 138221j,l; *17*, associated pygidium with single anterior pair of spines, ×5.4, U.S.N.M. 138221k; *19*, late meraspid cranidium, ×8, U.S.N.M. 138221a; *21,22,18*, series of early holaspid cranidia, ×8, ×10, ×8, U.S.N.M. 138221b,c,d; *14,15*, larger holaspid cranidia, ×7, ×6.3, U.S.N.M. 138221f,e; *16*, largest cranidium, a fragment, ×3, U.S.N.M. 138221g; *20,31*, associated librigenae, ×3, U.S.N.M. 138221h,i, all from NE–47.

24–30—Kendallina eryon (Hall). *24*, associated librigena, ×2.8, U.S.N.M. 138220e; *26,25*, associated pygidium and rubber mold from impression of 25, ×3, U.S.N.M. 138220f; *27*, largest cranidium, ×6.5, U.S.N.M. 138220c; *29,28,30*, series of small cranidia, ×9.3, ×6.5,×7.4, U.S.N.M. 138220a,d,c, all from NE-47.

32–35—Parabolinoides expansus Nelson. *32*, weathered cranidium, ×5, U.S.N.M. 138216, from 39–11. *33*, small cranidium from 39–16, ×4, U.S.N.M. 138215. *34,35*, profile and dorsal of largest cranidium from 39–12, ×3.5, ×3, U.S.N.M. 138217.

36—Pseudagnostus cf. *P. prolongus* (Whitfield). Single peeled cranidium, ×5.6, U.S.N.M. 138218, from NE–47.

37–40—Micromitra modesta (Lochman). *37*, small brachial valve from SM10, ×25, U.S.N.M. 138214. *38*, fragmentary pedicle valve from SM2, ×8, U.S.N.M. 138213. *39*, brachial valve from OC4, ×15, U.S.N.M. 138211. *40*, broken valve showing radiating ridges, ×10, U.S.N.M. 138212, from SM7.

41,42—Problematica I. Apical and profile view of single specimen, a crushed cone, ×4, U.S.N.M. 138219, from OC 10.

43,44—Lingulella sp. *43*, specimen with both valves viewed from brachial valve, ×8.3, U.S.N.M. 138206a; *44*, rubber mold of impression of interior showing radiating striae, ×8.4, U.S.N.M. 138206b, from NE–47.

45,49—Otusia sandbergi (Winchell). *45*, exterior of brachial valve, ×3, U.S.N.M. 138209a; *49*, exterior of pedicle valve, ×3, U.S.N.M. 138209b, from OC5.

46,47—Billingsella sp. exteriors of two fragmentary valves which appear to belong to this genus, ×3, U.S.N.M. 138207a,b, from 39–16.

48,50—cf. *Ocnerorthis cooperi* Bell. *48*, exterior of pedicle valve, ×1.8, U.S.N.M. 138208b; *50*, peeled pedicle valve, ×2.1, U.S.N.M. 138208a, from OC5.

51–53—Eoorthis remnicha (Winchell). *51*, small valve from OC10, ×1.6, U.S.N.M. 138230; *52,53*, large partially peeled valves from OC5, ×1, U.S.N.M. 138210a,b.

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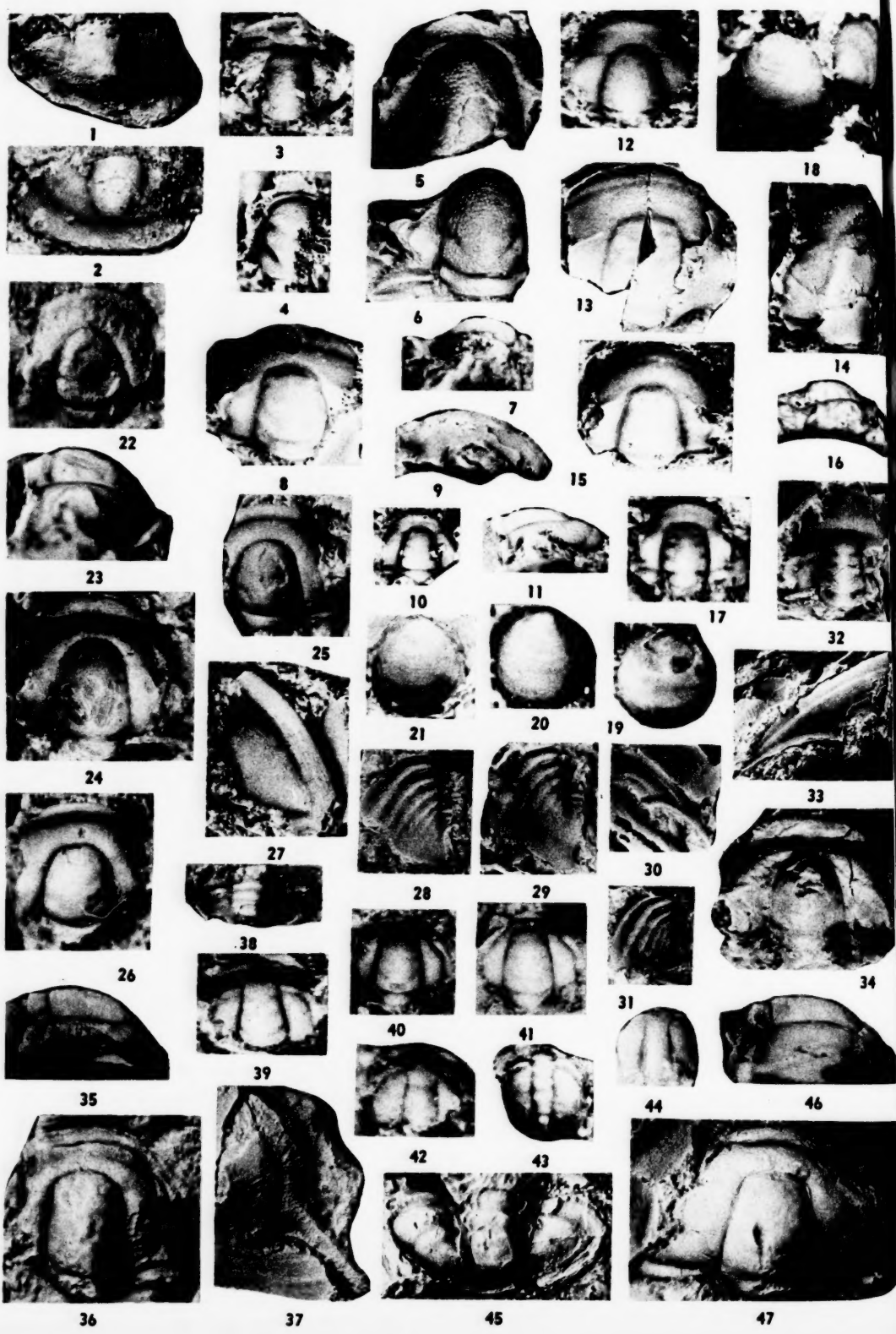
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the axis, along with all of Wyoming became emergent. Some portions stood higher than others during the Dresbachian-Franconian break since all along this axis as much as 100 to 150 feet of Dresbachian beds have locally been removed by erosion. The trend persisted through the Franconian also. It was not submerged until middle *Elvinia* zone time and then only shallowly as in the north it became the site of numerous *Collenia* reefs, during *Elvinia* zone time, and during the *Conaspis* zone furnished shallow hard bottoms for the only development of *Eoorthis* and *Billingsella* banks known in the northwest.

This positive axis appears to lie at the boundary between the stable shelf areas to the east and an extension of the miogeosyncline (an exogeosyncline) trending also northwest-southeast through southeast Idaho and northeast Utah. The area would appear to have been an unstable shelf region of differential movement between the slight downwarping of the shelf and the continuous downwarping of the exogeosyncline. In this boundary position rare extracratonic specimens were sporadically drifted into these shelf assemblages. The axis was apparently an early Paleozoic element persisting through the Devonian. Along its trend pre-Upper Devonian erosion cycles have cut deeper into the Cambrian beds than either to the west or to the east.

EXPLANATION OF PLATE 96

FIGS. *1,2*—*Housia* sp. Two weathered pygidia without the anchylosed anterior segment, ×1.4, ×5, U.S.N.M. 138199a,b, from 38–5.

3–7—*Burnetia* cf. *B. alta* Resser. *3,7*, dorsal, profile of small, best preserved cranidium, ×9, U.S.N.M. 138203b; *4,5*, fragments of two larger cranidia, ×3.4, ×4.3, U.S.N.M. 138203c,a, all from N1. *6*, largest broken cranidium, ×1.8, U.S.N.M. 138226, from 39–4.

8–17—*Camaraspis convexa* (Whitfield). *8,11*, dorsal, profile of peeled cranidium, ×3, U.S.N.M. 138228a; *15*, larger, more complete cranidium, ×3, U.S.N.M. 138228b, from 39–4. *10,17*, dorsal and *16*, profile, *12*, series of early holaspid cranidia, ×10, ×7.6, ×7.6, ×8, U.S.N.M. 138201b,c,d; *14*, large fragmentary cranidium, ×4, U.S.N.M. 138201e; *13,9*, dorsal, profile of largest cranidium, ×2.7, U.S.N.M. 138201a, all from N1.

18–21—*Linnarssonella girtyi* (Walcott). *18*, large brachial valve, and smaller pedicle valve, ×17, U.S.N.M. 138205a; *19*, partially exfoliated brachial valve, ×14, U.S.N.M. 138205b; *20*, pedicle valve, ×14, U.S.N.M. 138205c; *21*, brachial valve, ×13, U.S.N.M. 138205d, all from N1.

22–27—*Dellea suada* (Walcott). *22*, weathered cranidium from 38–5, ×4, U.S.N.M. 138227. *23,24*, profile, dorsal of medium-sized cranidium, ×4.4, U.S.N.M. 138200c; *25,26*, two smaller cranidia, ×4, ×4.4, U.S.N.M. 138200b,a; *27*, associated librigena, ×4.4, U.S.N.M. 138200d, all from N1.

28–33—*Pterocephalia bridgei* Resser. *28*, fragment of pygidium, *29*, rubber mold from impression of 28, ×2, U.S.N.M. 138204b; *31*, fragmentary pygidium, ×3, U.S.N.M. 138204c; *30,33*, associated librigenae, ×3, ×2, U.S.N.M. 138204d,e; *32*, cranidium, ×4, U.S.N.M. 138204a, all from N1.

34—*Deckera* cf. *D. completa* Wilson. The single cranidium, ×4.2, U.S.N.M. 138202, from N1.

35,36—*Kyphocephalus* sp. Profile, dorsal of weathered cranidium, ×3.7, ×4, U.S.N.M. 138195, from 38–5.

37—*Dokimocephalus* sp. Weathered librigena, ×2, U.S.N.M. 138196, from 38–5.

38–47—*Elvinia roemeri* (Shumard). *38*, small broken pygidium, ×4.4, U.S.N.M. 138197e; *43, 44,39*, series of meraspids, ×30, ×21, ×16, U.S.N.M. 138197a,b,c; *40*, early holaspid cranidium, *41*, rubber mold of impression of *40*, ×8.6, U.S.N.M. 138197d, all from N1. *42*, meraspid cranidium from 39–4, ×30, U.S.N.M. 138198; *45*, large weathered pygidium, ×1.5, U.S.N.M. 138229a; *46,47*, profile, dorsal of large weathered cranidium, ×2, U.S.N.M. 138229b, from 38–5.

SYSTEMATIC DESCRIPTIONS

Conaspis Zone

Phylum BRACHIOPODA

INARTICULATA

Superfamily OBOLACEA

LINGULELLA sp.

Pl. 95, figs. 43,44

Remarks.—A few valves of species of *Lingulella* were recovered. None of the specimens is complete. They appear to resemble most closely *L. perattenuata* (Whitfield) which occurs in the *Elvinia* zone and the lower part of the *Conaspis* zone in Montana and in Wisconsin. Better preserved material may demonstrate that this is also the species present in the Wyoming material.

Horizon and locality.—NE-47.

Figured specimens.—Two valves, U.S.N.M. 138206a,b.

ARTICULATA

Superfamily ORTHACEA

BILLINGSELLA sp.

Pl. 95, figs. 46,47

Remarks.—Two small valves are tentatively referred to this genus on the basis of their external appearance. They occur in a small collection at the top of the Cambrian in the Sheep Mountain section and probably come from the *Billingsella* subzone, representing the same horizon as OC6 in the Clear Creek section. In the latter section the shells are silicified and have been etched and are being studied by W. C. Bell.

Horizon and locality.—39-16.

Figured specimens.—Valves, U.S.N.M. 138207a,b.

EOORTHIS REMNICHA

(N. H. Winchell)

Pl. 95, figs. 51–53

Orthis remnicha N.H. Winchell, 1886, p. 317, pl. 2, fig. 7.

Eoorthis remnicha (N. H. Winchell) Walcott, 1912, p. 786–787, pl. 91, figs. 1,1a–s; pl. 92, figs. 2,2a–d,3,3a–e (synonymy to date); Bell, 1941, p. 254, pl. 36, figs. 14–23 (synonymy to date); Shimer and Shrock, 1944, p. 295, pl. 110, figs. 29–33.

Remarks.—A large number of valves of *Eoorthis* occur in the Clear Creek section between 18 and 20 feet below the base of the Bighorn. The horizon is apparently a development of the *Eoorthis subzone.* This subzone was first widely recognized in the Upper Mississippi valley sections, and subsequently noted in Texas but has not previously been recognized in the Montana-Wyoming area. In this material the valves are very abundant and range up to over 1 inch in length. But the subzone appears to be rather thin as this particular collection came from a single bed; and in the Clear Creek section this was all the material which was available. A second collection (OC10) appears to represent approximately the same horizon, but it is a bioclastic limestone obtained from a locality approximately one-fourth mile from OC5. The second collection came from a single bed about 6 inches thick. At present it would appear that the *Eoorthis* subzone is a local development in this area and could not be over 1 foot in thickness.

Horizon and locality.—OC5, OC10.

Figured specimens.—Valves, U.S.N.M. 138210a,b—OC5; valve, U.S.N.M. 138230—OC10.

OTUSIA SANDBERGI (Winchell)

Pl. 95, figs. 45,49

Orthis sandbergi Winchell, 1886, p. 318, pl. 2, figs. 8,9.

Otusia sandbergi (Winchell) Walcott, 1912, p. 769, pl. 93, figs. 4,4a–d (synonymy to date); Bell, 1941, p. 251, pl. 37, figs. 1–5.

Remarks.—A small number of valves of this species occur associated with the numerous *Eoorthis* valves. This is the same association as is recorded for the species at the type locality at Red Wing, Minnesota. The specimens are easily distinguished from the *Eoorthis* valves by their small size, neat alate shape and distinctive ornamentation. The species definitely appears to be associated only with the *Eoorthis* subzone assemblage in this section, and when more is known about it, may prove to be another significant biostratigraphic form. A brachial and a pedicle valve are figured for reference.

Horizon and locality.—OC5.

Figured specimens.—Brachial valve, U.S.N.M. 138209a; pedicle valve, U.S.N.M. 138209b.

cf. OCNERORTHIS COOPERI Bell

Pl. 95, figs. 11,48,50

Remarks.—A small number of shells in the *Eoorthis* subzone assemblage may belong to

this species. The exterior appearance is most similar to this species but none of the valves show interiors well enough preserved to make identification of the species certain. Their occurrence in the *Eoorthis* assemblage is noted, since the exact biostratigraphic range of *Ocnerorthis* has not yet been determined. When the genus was described, it was only known that it was probably early Franconian in age. Subsequently Grant (1958) found *Ocnerorthis monticola* Bell associated with the *Elvinia* zone assemblage, and in this Wyoming material the authors also have definite association of *Ocnerorthis cooperi* Bell with a trilobite assemblage from the upper part of the *Elvinia* zone.

Horizon and locality.—OC5, OC10.

Figured specimens.—Valves, U.S.N.M. 138208a,b—OC5; valve, U.S.N.M. 138225—36-16.

TRILOBITA

Family PARABOLINOIDIDAE

PARABOLINOIDES EXPANSUS Nelson

Pl. 95, figs. 32–35

Parabolinoides expansa Nelson, 1951, p. 776, pl. 107, figs. 1,3; Berg, 1953, p. 564 (in synonymy of *P. contractus* Frederickson).

Remarks.—Only five poorly preserved cranidia of *Parabolinoides* were obtained from the *Conaspis* zone material. The three best preserved cranidia can be definitely assigned to *P. expansus* Nelson which they resemble in the diverging anterior branches of the facial sutures, the distinctly downsloping preglabellar field, and the horizontal, slightly convex anterior border. The cranidia come from three separate, but closely spaced (stratigraphically) collections.

Two other cranidial fragments from horizon OC5 can be assigned to *Parabolinoides*, but on both of them the preglabellar area appears to be only very slightly downsloping and the anterior border slightly convex and horizontal. These two features are the distinguishing characteristics of *P. contractus* Frederickson, and it may be that these fragments do represent a second species but their preservation is so poor these features may be entirely illusory.

Horizon and locality.—36-11, 36-12, 36-19, OC5?

Figured specimens.—Cranidium, U.S.N.M. 138216—39-11; cranidium, U.S.N.M. 138217—39-12; cranidium, U.S.N.M. 138215—39-19.

KENDALLINA ERYON (Hall)

Pl. 95, figs. 24–30

Conocephalites eryon Hall, 1863, p. 157, pl. 7, figs. 10–16, pl. 8, figs. 16,31.
Kendallia eryon (Hall) Raasch, 1939, p. 94; Berg, 1953, p. 562–563, pl. 59, fig. 9, pl. 60, fig. 1 (synonymy to date).
Kendallina eryon (Hall) Berg, 1959.

Remarks.—Three small but distinctive cranidia, one fragmentary pygidium of medium size and a librigena are referred to this species. The identification of the material was verified by comparison with limestone specimens of the species from Montana, as the limestone preservation gives a clear picture than the sandstone material from Wisconsin. One of the cranidia shows at least two pairs of faint glabellar furrows. The associated librigena is quite smooth.

The associated pygidium is subcircular with a broad, slightly tapered axis with four axial rings and terminal, narrow pleural platforms, and a narrow, flat border. This appears to be the same type of pygidium as the poorly preserved specimen figured by DeLand and Shaw, 1956, pl. 67, fig. 4, as *T. cordillerensis* from Sweetwater Canyon, Wyoming.

Horizon and locality.—NE-47.

Figured specimens.—Cranidia, U.S.N.M. 138220a–d; librigena, U.S.N.M. 138220e; pygidium, U.S.N.M. 138220f.

TAENICEPHALUS SHUMARDI (Hall)

Pl. 95, figs. 12-23,31

Conocephalites shumardi Hall, 1863, p. 154, pl. 7, figs. 1,2, pl. 8, fig. 32.
Taenicephalus shumardi (Hall) Walcott, 1924, p. 59, pl. 13, fig. 1; Wilson, 1951, p. 652–653, pl. 95, figs. 21–23,25 (synonymy to date); Berg, 1953, p. 565, pl. 59, figs. 11–14.
Taenicephalus cordillerensis DeLand and Shaw, 1956 (not Miller), p. 559, pl. 67, fig. 3 (additional synonymy to date).

Remarks.—A small number of cranidia which show a size range from late meraspid to holaspid stage about 7 mm. in length, four associated librigenae and several associated pygidia have been assigned to this species. The cranidia all show the accepted diagnostic features of the species: 1) base of the glabella wider than length, 2) sharply truncate glabellar front, 3) cranidium narrower across palpebral lobes than the sag.

length. The outer surface of the exoskeleton appear finely granular.

The correctly associated pygidium of *Taenicephalus* is not definitely known. Hall assigned a subcircular pygidium to his type cranidia, and Grant (1958) has found a similar pygidium in some of his material from southwestern Montana. Miller (1936b) associated a transverse pygidium with 3 axial rings and slightly tapered axis with his species. Grant has also associated this type pygidium with *T. shumardi* cranidia in Montana. In the *Conaspis* zone material from Clear Creek two types of pygidia were also obtained. The subcircular type we have associated with *Kendallina* and have referred a narrowly transverse pygidium with a broad bluntly rounded axis with 3 axial rings to *T. shumardi.* The three fragmentary pygidia of this type show a border variation which cannot be attributed to size. Two of the specimens show three broad pleurae with three pairs of very short pointed marginal spines. On the other pygidium the narrow marginal border is complete except for a small notch opposite the anterior pleurae. On all specimens a narrow but distinct border furrow separates off the border.

Horizon and locality.—NE-47.

Figured specimens.—Cranidia, U.S.N.M. 138221a–g; librigenae, U.S.N.M. 138221h,i; pygidia, U.S.N.M. 138221j,l,k;

Order AGNOSTIDA
PSEUDAGNOSTUS sp. cf. P. PROLONGUS
(Hall & Whitefield)
Pl. 95, fig. 36

Agnostus prolongus Hall and Whitfield, 1877, p. 230, pl. 1, figs. 30,31.
Pseudagnostus prolongus (Hall and Whitfield) Palmer, 1955, p. 98, pl. 19, figs. 17,18,22.

Remarks.—Palmer (1955) describes this species as similar to *P. communis* (Hall and Whitfield) but with very poorly defined axial furrows on the exterior. A single weathered and exfoliated cephalon was obtained from the *Conaspis* zone material. The furrows on the interior are distinguishable but shallow and appear to have about the same depth as the exfoliated cephalon illustrated (pl. 19, fig. 22) by Palmer (1955).

Horizon and locality.—NE-47.

Figured specimen.—Cephalon, U.S.N.M. 138218.

Incertae Sedis
Problematica I
Pl. 95, figs. 41,42

Remarks.—A single specimen of a small cone-shaped body, 3 mm. high at the apex and 5.5 mm. wide was obtained. The specimen has apparently been crushed down and partly broken and then worn off at the apex before burial. It lies now with the damaged apex up and the wider apertural? part down. The shape suggests either a gastropod or a simple cup coral, but the material of the specimen is a thick crystalline calcite resembling Echinodermata plates. The outer surface is covered with very fine concentric striae paralleling the wider apertural? side.

Horizon and locality.—OC10.

Figured specimen.—U.S.N.M. 138219.

Elvinia Zone
Family DOKIMOCEPHALIDAE
BURNETIA sp. cf. B. ALTA Resser
Pl. 96, figs. 3–7

Burnetia alta Resser, 1942, p. 80, pl. 17, figs. 12–14; DeLand and Shaw, 1956, p. 548, pl. 65, figs. 1–3.

Remarks.—Fragmentary *Burnetia* cranidia occur in two collections. Only one small cranidium has the frontal area complete. This specimen has a narrow preglabellar field, a distinct transverse anterior border furrow, and an anterior border of moderate length (sag) and subequal (tr) width. These features are characteristic of *B. alta* described by Resser from the Davis formation of Missouri. The species has also been recorded from Steele Butte, Wyoming by DeLand and Shaw. The small cranidia in this material have only a moderately convex glabella, but the glabella in the largest fragment is more strongly convex and the specimen more nearly approaches Resser's type in size.

Horizon and locality.—N1, 39-4.

Figured specimens.—Cranidium, U.S.N.M. 138226—39-4; cranidia, U.S.N.M. 138203a,b,c—N1.

DECKERA sp. cf. D. COMPLETA Wilson
Pl. 96, fig. 34

Deckera completa Wilson, 1951, p. 634, pl. 90, figs. 10–17.

Remarks.—The single broken and weath-

ered cranidium of *Deckera* is referred to *D. completa* Wilson described from Pennsylvania. Wilson states that the characteristics of *D. completa* are a preglabellar field: anterior border ratio of about 1:1; librigenae rising from the dorsal furrow at an angle of about 35°; and granules on the glabellar slopes. Wilson also states that he has observed fragmentary cranidia of *Deckera* from Texas with the same ratio. On the Wyoming cranidium the preglabellar field: anterior border ratio is 1:1, but the weathered condition of the surface prevents accurate determination of the other two features. Certainly the cranidium does not represent *D. aldenensis* Frederickson, the genotype from Oklahoma in which the preglabellar field: anterior border ratio is 1:2. When more complete specimens can be obtained from this region, it is quite possible that this specimen may represent a distinct species.

Horizon and locality.—N1.

Figured specimen.—Cranidium, U.S.N.M. 138202.

Dokimocephalus sp.
Pl. 96, fig. 37

Remarks.—A single moderately well preserved librigena has the laterally projecting genal spine and short quadrate ocular platform which is especially characteristic of this genus. Specific identification is not possible.

Horizon and locality.—38-5.

Figured specimen.—Librigena, U.S.N.M. 138196.

Kyphocephalus sp.
Pl. 96, figs. 35,36

Remarks.—Two very poorly preserved cranidia appear to belong to this genus but cannot be identified specifically. The best preserved specimen is figured. The specimen shows the elongate parallel-sided glabella so characteristic of the genus. The continuously downsloping preglabellar field and anterior border, and the apparent greater width (sag) of the preglabellar field suggest that these specimens may represent *K. bridgerensis* Miller described from Dry Creek, Fremont County, Wyoming. But the anterior border is damaged so that its correct width (sag) cannot be determined.

Horizon and locality.—38-5.

Figured specimen.—Cranidium, U.S.N.M. 138195.

Family Marjumiidae
Dellea suada (Walcott)
Pl. 96, figs. 22–27

Ptychoparia suada Walcott, 1890, p. 274, pl. 21, fig. 9.

Dellea suada (Walcott) Wilson, 1951, p. 636, pl. 91, figs. 4–10,18,20–23,25,26 (complete synonymy to date); DeLand and Shaw, 1956, p. 554, pl. 66, figs. 8,9.

Remarks.—Three deeply weathered cranidia from 38-5 have been tentatively assigned to this species, and four broken but better preserved cranidia and 2 librigenae from N1 are definitely assigned. All the cranidia are about the same size, ranging from 5 to 7 mm. in length, but the smallest is only 1.5 mm. The outer surface on some of the specimens is well enough preserved to show the fine granular surface on the glabella and fixigenae and narrow transverse ridges on the anterior border.

Horizon and locality.—38-5, N1.

Figured specimens.—Cranidium, U.S.N.M. 138227—38-5; librigena, U.S.N.M. 138200d; cranidia, U.S.N.M. 138200a,b,c—N1.

Family Pterocephaliidae
Camaraspis convexa (Whitfield)
Pl. 96, figs. 8–17

Arionellus (*Agraulos*) *convexus* Whitfield, 1878, p. 57.

Agraulos cushingi Ruedemann, 1916, p. 89, pl. 30, figs. 1,2,4.

Camaraspis convexus (Whitfield) Ulrich and Resser in Ulrich, 1924, p. 94; Wilson, 1951, p. 630, pl. 90, figs. 1–8 (synonymy to date).

Remarks.—Some small and medium-sized cranidia from three collections have been assigned to this species. Most of the specimens are peeled so that on them the axial and anterior border furrows, the eye ridges, and the glabellar furrows are more distinct than on the unpeeled specimens. This feature is especially noticeable in the smaller cranidia. In profile the cranidia show a moderate convexity which has led to their assignment to the species. DeLand and Shaw have figured cranidia of *Camaraspis* from Steele Butte, Wyoming which they assign to *C. plana*. The cranidia are rather smooth, but as a profile is not figured their convexity cannot be determined.

Camaraspis convexa (Whitfield) has been recognized in Pennsylvania, throughout the Mississippi valley, in Montana as well as Wyoming and is considered to be the characteristic form of the *Camaraspis* subzone of the upper part of the *Elvinia* zone.

Horizon and locality.—39-4, N1, 38-5.

Figured specimens.—Cranidia, U.S.N.M. 138201a–e—N1; cranidia, U.S.N.M. 138228a,b—39-4.

Pterocephalia bridgei Resser
Pl. 96, figs. 28–33

Pterocephalia bridgei Resser, 1938, p. 40.
Pterocephalia bridgei Resser, Lochman, 1950, p. 334, pl. 47, figs. 14–18 (synonymy to date).

Remarks.—A single small cranidium, and several fragmentary librigenae and pygidia are referred to this species. The anterior margin on the single cranidium is not complete so that the measurement of the exact length (sag) is not possible. However, the proportions of the sag. length of the frontal area to the sag. length of the glabella and occipital ring are most similar to those found in *P. bridgei*.

Horizon and locality.—N1

Figured specimens.—Cranidium, U.S.N.M. 138204a; pygidia, U.S.N.M. 138204b,c; librigenae, U.S.N.M. 138204d,e.

Family Solenopleuridae
Cliffia lataegenae (Wilson)
Pl. 95, figs. 1–7

Acrocephalites lataegenae Wilson, 1949, p. 31, pl. 10, fig. 14.
Cliffia lataegenae (Wilson), DeLand & Shaw, 1956, p. 551, pl. 65, figs. 11,12 (synonymy to date).

Remarks.—A few cranidia, pygidia and librigenae belonging to this species were obtained from two collections from the *Elvinia* zone. The collections are all limited in material, so that the appearance of specimens in several collections suggests that the species must actually have been a rather abundant form in the *Elvinia* assemblages of this region.

Horizon and locality.—39-4, N1.

Figured specimens.—Cranidia, librigenae, U.S.N.M. 138223a–d—N1; cranidium, pygidium, U.S.N.M. 138222b,a—39-4.

Family Elviniidae
Elvinia roemeri (Shumard)
Pl. 96, figs. 38–47

Dikelocephalus roemeri Shumard, 1861, p. 220.
Elvinia roemeri (Shumard) Walcott, 1924, p. 56, pl. 11, fig. 3; Frederickson, 1949, p. 352, pl. 69, figs. 19–21 (for synonymy to date); Lochman, 1950, p. 333, pl. 47, figs. 21–23; Wilson, 1951, p. 624, pl. 92, figs. 18–22; Nelson, 1951, p. 775, pl. 107, fig. 8.

Remarks.—This species is represented by a single crushed and weathered but essentially complete cranidium and pygidium from one collection which consists of a coquina of badly broken trilobite exoskeletons and valves of *Linnarssonella*. From another collection several meraspid cranidia and an early holaspid cranidium were obtained. On these specimens the palpebral rims and eye ridges are very distinct and the palpebral lobes are proportionately somewhat longer than on the large adult cranidia. In the latest meraspid cranidium the preglabellar area is very narrow (sag) and the glabellar furrows are all incomplete.

Locality and Horizon.—38-5, N1, 39-4.

Figured specimens.—Large cranidium and pygidium, U.S.N.M. 138229b,a—38-5; meraspid cranidium, U.S.N.M. 138198—39-4; meraspid and holaspid cranidia, pygidium, U.S.N.M. 138197—N1.

Family Housiidae
Housia sp.
Pl. 96, figs. 1,2

Remarks.—Four deeply weathered pygidia from one collection can be referred to this genus. The specimens vary in size from a large pygidium 22 mm. in width × 11 mm. in length to the smallest, 4 mm. in width × 2.5 mm. in length.

Horizon and locality.—38-5

Figured specimens.—Pygidia, U.S.N.M. 138199a,b.

Phylum Brachiopoda
Class Inarticulata
Order Neotremata
Superfamily Acrotretacea
Linnarssonella girtyi Walcott
Pl. 96, figs. 18–21

Linnarssonella girtyi Walcott, 1902, pp. 602–602; Walcott, 1912, p. 666, pl. 78, figs. 5,5a, pl. 79, figs. 1,1a–r; Shimer and Shrock, 1949, p. 289, pl. 109, figs. 4–8.

Remarks.—This species is represented by a very large number of valves scattered among the trilobite hash which makes up the limestones of the collections from the *Elvinia* zone. The *Linnarssonella* valves are small and fragile, but almost all of them are complete. Such good preservation suggests that they grew attached to the broken trilobite exoskeletons which formed the debris piles scattered over an otherwise soft mud or ooze bottom. A few valves have the exterior shell layers somewhat removed so that some of the internal muscle scars can be distinguished.

Horizon and locality.—N1, 38-5, OC5.

Figured specimens.—Valves, U.S.N.M. 138205a–d—N1.

CLASS ARTICULATA
Superfamily ORTHACEA
OCNERORTHIS COOPERI Bell
Pl. 95, figs. 8–11

Ocnerorthis cooperi Bell, 1941, p. 252, pl. 37, figs. 18–25; Shimer and Shrock, 1949, p. 293, pl. 110, figs. 22–25.

Remarks.—Two ventral and three dorsal valves were obtained from the collections of the *Elvinia* zone. The outer surfaces are weathered and only one interior is known, but they appear definitely assignable to the genus and most closely resemble Bell's genotype, *O. cooperi.* Grant (1958) had obtained *O. monticola* Bell from the upper part of the *Elvinia* zone in both Montana and Wyoming, and *O.? iddingsi* (Walcott) from the Dry Creek shale must also belong in the *Elvinia* zone. The exact horizon of the type material is not known. The probable identity of these Wyoming specimens with the types, which come from Torrey Creek, Wind River Range, Wyoming, suggests that the genus may be characteristic of the *Elvinia* zone throughout this area.

Horizon and locality.—N1, 38-5.

Figured specimens.—Valves, U.S.N.M. 138224a–c—N1; valve, U.S.N.M. 138225—38-5.

Aphelaspis Zone
Family CATILLICEPHALIDAE
GLAPHYRASPIS OCCIDENTALIS Lochman
Pl. 97, figs. 1–8

Raaschella occidentalis Lochman in Lochman and Duncan, 1944, p. 43–44, pl. 4, figs. 1–5.
Raaschella occidentalis Lochman, Shaw, 1956a, p. 51, pl. 12, figs. 4,5.

Remarks.—This species is the most abundant form in the small *Aphelaspis* faunule obtained and is represented by 10 cranidia, two fragmentary pygidia and several librigenae. Most of the specimens are peeled but some of the cranidia retain patches of the outer surface and on the librigenae it is well preserved. The largest cranidium measures 3.25 mm. in length, and most are 3 mm. in length which seems to be the standard adult size for the cranidium.

In this material the cranidia show some variation in the shape of the glabella from a shorter, broad type to a somewhat longer type. The single cranidium figured by Shaw from Steele Butte shows the long type glabella, while the holotype from Montana has a slightly shorter type. This feature definitely seems to be an intraspecific variation within the populations of this species in the Cordilleran region. Both types are figured in this paper.

Horizon and locality.—OC1a.

Figured specimens.—Cranidia, U.S.N.M. 137957a–d; librigena, U.S.N.M. 137957g; pygidia, U.S.N.M. 137957e–f.

Family CHEILOCEPHALIDAE
CHEILOCEPHALUS sp. undet.
Pl. 97, figs. 11–13

Remarks.—This genus is represented in the *Aphelaspis* faunule by two fragmentary cranidia, a fragmentary pygidium and one small, nearly complete pygidium with well preserved outer surface. On this specimen the pleural furrows and interpleural grooves are well defined on the pleural fields and continue across the downsloping border nearly to the outer margin. The outer surface is densely and finely granular. In the greater length of the axis and more trigonal shape this pygidium most closely resembles that of *Cheilocephalus breviloba* (Walcott) from Texas and the southern Appalachians rather than that of *C. delandi* Shaw from Steele Butte, Wyoming. The figured specimens of the latter species are all quite large, and consequently the possibility of change of shape with increase in size cannot be elimiated from consideration. It is considered best not to assign a specific determination until more and better material is available.

Horizon and locality.—OC1a.

Figured specimens.—Cranidium, U.S.-

N.M. 137959c; pygidia, U.S.N.M. 137959a,b.

Phylum GASTROPODA
HYPSELOCONUS SIMPLEX Lochman
Pl. 97, figs. 9,10

Hypseloconus simplex Lochman in Lochman and Duncan, 1944, p. 42, pl. 4, fig. 6.
Hypseloconus simplex simplex Lochman, Shaw, 1956a, p. 51, pl. 12, fig. 7, pl. 13, fig. 3.

Remarks.—Two small steinkerns, 12 mm. in height by 7 mm. across at the aperture, were obtained from the *Aphelaspis* zone faunule. The best preserved specimen shows four faint rounded transverse ridges crossing the shell and thus in markings and dimensions is very similar to the Montana holotype. Shaw recognized several subspecies based on the amount of curvature near the apex of the shell. These specimens, though broken, do not seem to differ from the holotype in this respect. The rather persistent occurrence of gastropod specimens in the *Aphelaspis* faunules of Montana and Wyoming and their absence from the much larger faunules of this age described by Palmer (1954) from Texas indicates that at least these members of this phylum were already adapted to particular habitats.

Horizon and locality.—OC1a.

Figured specimen.—Steinkern, U.S.N.M. 137958.

Crepicephalus Zone
Family COOSELLIDAE
COOSINA ARISTON (Walcott)
Pl. 97, figs. 15–20

Maryvillia ariston Walcott, 1916, p. 401, Pl. 64, figs. 5,5′ (not 5a).
Coosina ariston Walcott, Rasetti, 1956, p. 1267–1268 (complete synonymy to date).

Remarks.—Several fragmentary cranidia and pygidia, one a small specimen, 1.25 mm. in length, are tentatively referred to this species as no marked differences in the Wyoming specimens (allowing for the poor preservation) can be observed. The pygidium 1.25 mm. in length is the smallest identified for the genus to date. On it 7 axial segments and a terminal portion, and 6 pleural segments can be distinguished, a larger number than has been observed on the large pygidia. On this specimen also the interpleural grooves are more distinct than on most specimens.

Horizon and locality.—OC1b.

Figured specimens.—Cranidia, U.S.N.M. 137961a,b; pygidia, U.S.N.M. 137961c,d.

Family TRICREPICEPHALIDAE
TRICREPICEPHALUS sp. undet.

Remarks.—A single fragmentary librigenae belonging to this genus was obtained from the very small *Crepicephalus* assemblage from the Clear Creek section. No cranidia or pygidia could be associated with it.

Horizon and Locality.—OC1b.

Family CREPICEPHALIDAE
UNCASPIS sp. undet.
Pl. 97, fig. 14

Remarks.—One poorly preserved pygidium can be referred to this genus with certainty. It consists of most of the axis and the right pleural region which shows the characteristic narrow pleural field, the narrow downsloping border with a flattened, apparently short postero-lateral spine.

Horizon and locality.—OC1b.

Figured specimen.—Pygidium, U.S.N.M. 137960.

cf. Basal *Crepicephalus* Zone
Family LECANOPYGIDAE
MINICEPHALUS n. gen.

Opisthoparian isopygous exoskeleton; glabella conical, lateral furrows faint to obsolete, dorsal furrow distinct, frontal area narrow (sag) crossed by distinct anterior border furrow, anterior and lateral borders marked by narrow parallel imbricating ridges; fixigenae about 0.5 glabellar width, palpebral lobes medium size, posterior to center of glabella, narrow posterior area; librigenae short, wide, with rounded genal angle. Thorax not known.

Pygidium narrow-transverse, axis convex, tapered only slightly to rounded end, continuing as low post-axial ridge 0.5 or more across posterior border; 3 axial rings and terminal portion, pleural regions wider than axis, regularly convex, 3 broad pleurae, broad shallow interpleural grooves, faint to obsolete pleural furrows, faint border furrow.

Outer surface finely reticulate, anterior and lateral borders of cephalon crossed by

many distinct narrow imbricating ridges, inner surface punctate.

Genotype.—*Minicephalus primus*, n. sp.

Remarks.—The discovery of this form in a *Crepicephalus* assemblage is surprising. The genus appears in the structure of the exoskeleton to be a member of the Lecanopygidae which are not known again in the North American cratonic assemblages until near the end of the Franconian stage, and become more prominent in the Trempealeauan faunas. The distinct punctate inner surface and finely reticulate outer surface of the exoskeleton are quite unusual features for a member of the *Crepicephalus* assemblage, but not uncommon in the Trempealeauan genera.

MINICEPHALUS PRIMUS, n. sp.
Pl. 97, figs. 42–52

Cephalon narrowly ovoid, glabella conical, moderately convex, dorsal furrow shallow on exterior, deep on interior, no lateral furrows, occipital furrow broad, distinct, occipital ring low, subtrigonal, preglabellar field narrow, vertical in adult, broad deep anterior border furrow, medium-wide anterior border curves up from furrow, then down vertically to anterior margin, crossed by low longitudinal ridges; fixigenae upsloping, convex, anterior area medium-width (tr); steeply downsloping, no eye ridge, palpebral area 0.5 glabellar width, palpebral furrow almost obsolete, palpebral lobe medium-size, posterior to center of glabella, posterior area narrow, same width (tr) as occipital ring, narrow posterior furrow; librigenae short, broad, steeply sloping, deep lateral border furrow shallows posteriorly, moderately wide vertical border, crossed by low parallel ridges, short rounded genal angle.

Pygidium narrow-transverse, regularly convex; axis of medium width and convexity, narrower (tr) than pleural region, extending over 0.66 length with rounded end, then continuing in a low postaxial ridge halfway across posterior border, two broad shallow anterior axial furrows on exterior—on interior 3 rings and terminal portion, dorsal furrow broad, shallow, at sides only, pleural regions regularly convex, only anterior interpleural groove distinct on exterior, faint second and third grooves may appear on interior, pleural furrows obsolete, border furrow broad, faint, border medium-width, convex.

Outer surface covered by fine reticulate pattern of minute raised ridges (may appear as rows of minute granules) with border of cephalon crossed by narrow longitudinal ridges; inner surface punctate.

Remarks.—This species is represented by one small (1.75 mm. in length) and four larger cranidia (up to 8 mm.), two librigenae and 13 pygidia (from 3.5 to 12 mm. in width (tr)). The pygidia show no significant structural changes throughout their size range, but the small cranidium has horizontal fixigenae, a gently downsloping preglabellar field, narrow anterior border furrow and moderately convex anterior border. The vertical position of the frontal area occurs in all the larger cranidia.

The small representation of the species is attributed to the small size of the collection. This species and *Tricrepicephalus* cf. *coria* are the most abundantly represented members of the faunule, and it is concluded that *M. primus* must have been a normal member of the basal *Crepicephalus* zone faunule in this region.

Horizon and Locality.—OC2.

Types.—Holotype, cranidium; U.S.N.M. 137971; paratypes, cranidia, U.S.N.M. 137972a,d; librigenae, U.S.N.M. 137972b; pygidia, U.S.N.M. 137972e,f,g.

Family TRICREPICEPHALIDAE
TRICREPICEPHALUS sp. cf. T. CORIA Walcott
Pl. 97, figs. 21–26

Crepicephalus coria Walcott, 1916, p. 206, pl. 33, figs. 3,3a–3g.

Tricrepicephalus coria (Walcott) Palmer, 1954, p. 755, pl. 81, figs. 1–4,6 (Palmer's synonymy to date).

Remarks.—Fragmentary cranidia and pygidia, several librigenae and thoracic segments are referred to this species. The large coarse granules (with a central hollow) are well preserved on the outer surface of the specimens and, in addition, the surface shows granules of two smaller sizes interspersed among the larger granules. The granules are arranged in rows across the axial rings of the pygidium.

Palmer (1954) referred seven other species described from various parts of the

country to *Tricrepicephalus coria*. He does state, however, that he thinks his large grouping of species "probably represents a species group rather than a single species in a strict biological sense," although he always refers to it as a single species. Palmer's definition of the diagnostic characteristics of *Tricrepicephalus coria* appears to have been obtained entirely by expanding the description from that of the original Utah specimens into a blanket definition including all the features of all the species he has placed in synonymy, rather than from a population study of *T. coria*. According to published records the Utah species of *T. coria* is still known only from Walcott's original material. The cotype cranidia show the narrow, slit-like pits in the anterior border furrow, but they do not appear to have the somewhat pointed (nasute) anterior border as seen on these Wyoming specimens and on some of Palmer's specimens (1954, pl. 81, fig. 3). The Wyoming material is too limited and incomplete for a population study.

Horizon and locality.—OC2.

Figured specimens.—Cranidia, U.S.N.M. 137962a,b; librigenae, U.S.N.M. 137962c,d; pygidia, U.S.N.M. 137962e,f.

Family COOSELLIDAE
cf. COOSINA sp. undet.
Pl. 97, figs. 29–31

Remarks.—Two pygidia are referred to *Coosina*. One is a small complete specimen, 1.5 mm. in length, which is exactly the same shape as the small specimen from OC1b but the surface is nearly smooth. This may be caused by wear. The second pygidium is somewhat larger but badly broken so that accurate specific identification is not possible. It may be that both or just the small pygidium represent the presence of *Coosina ariston* (Walcott) in this lower horizon.

Horizon and locality.—OC2.

Figured specimens.—Pygidia, U.S.N.M. 137964a,b.

Family ASAPHISCIDAE
Subfamily BLOUNTINAE
MARYVILLIA sp. undet.
Pl. 97, figs. 27,28

Remarks.—Two pygidia, both peeled specimens, can be referred to *Maryvillia*, but they do show some differences when compared with the pygidia referred to *M. arion* Walcott and *M. eleanora* (Lochman) described from a comparable horizon in Montana. Shaw did not record this genus from Steele Butte, Wyoming.

The features characteristic of these specimens seem to place them half way between the two Montana species. The axis extends a short distance beyond the trace of the border furrow, but not as far as in *M. arion*. The axis shows 8 axial rings and a narrow terminal portion. In the smaller number of axial rings it is most similar to *M. eleanora* (Lochman).

Horizon and locality.—OC2.

Figured specimens.—Pygidia, U.S.N.M. 137963a,b.

Family CATILLICEPHALIDAE
LONCHOCEPHALUS sp. undet.
Pl. 97, fig. 32

Remarks.—A single well preserved pygidium belongs to this genus, but until a cranidium can be associated with it a specific determination cannot be made.

The specimen is 1.5 mm. in length by 2.75 mm. in width with a distinct triangular outline. The axis is divided into 4 or 5 axial rings and a narrow terminal portion. The gently sloping pleural fields show 4 broad pleurae separated by broad deep interpleural grooves ending abruptly at the low rim which defines the change in slope to the narrow vertical border. The pleural furrows are shallow. The outer surface appears smooth.

The pygidium is not like that assigned to *L. montanensis* Lochman but is more similar in its triangular outline to that of the genotype, *L. chippewaensis*, from Wisconsin. However, two species of *Lonchocephalus* have been described from the House Range, Utah based on cranidia only, and it is quite possible that this pygidium may represent one of these forms.

Horizon and locality.—OC2.

Figured specimen.—Pygidium, U.S.N.M. 137965.

Phylum BRACHIOPODA
cf. BILLINGSELLA sp. undet.
Pl. 97, figs. 40,41

Remarks.—Four fragmentary limestone molds of the interior of the shell of an artic-

ulate brachiopod have been tentatively referred to *Billingsella*. Rare specimens of this genus have been recorded from a Dresbachian faunule from the Riley formation of central Texas and in the basal *Crepicephalus* faunule from Half Moon Pass section in Montana. Bell (in Lochman and Duncan, 1944) comments on the scarcity of the calcareous brachiopods in the Dresbachian faunas of the west, in view of their abundance in the Middle Cambrian assemblages and again in the Franconian faunas. This scarcity would appear to be a reflection of adverse ecologic conditions. There is a significant percent of clay and silt in the Dresbachian rocks of Montana and Wyoming. The silting in of shore areas may well have produced stagnant or semi-stagnant water conditions in many localities.

Horizon and locality.—OC2.

Figured specimens.—Internal molds, U. S.-N.M. 137970a,b.

Phylum GASTROPODA
SEMICIRCULAREA ARCUATA Lochman
Pl. 97, figs. 33,34

Semicircularea arcuata Lochman in Lochman and Duncan, 1944, p. 81, pl. 12, figs. 22–27.

Remarks.—This species is represented by 11 specimens ranging in size from 1.25 mm. in height by 1 mm. across the aperture to 2.75 mm. by 2.25 mm. Most of the specimens are steinkerns, many showing the low median infold on each side of the shell quite clearly. Only one or two specimens still retain an indication of the fine transverse ridges of the outer surface ornamentation of shell.

The species is very abundant in and ranges throughout the upper half of the *Cedaria* zone. Its occurrence in this basal *Crepicephalus* faunule appears to be near the end of its stratigraphic range.

Horizon and locality.—OC2.

Figured specimens.—U.S.N.M. 137966a,b.

Cedaria Zone
Calcareous Algae
Pl. 98, figs. 57–59

Remarks.—A small number of specimens from three horizons appear to represent the same form which was so identified by Lochman from the basal Bonneterre fauna of Missouri. The specimens range in size from 0.5 mm. to 2.5 mm., show the very characteristic pear-shaped body tapered to a point at one end, broadly rounded at the other end with a central circular marking on the slightly flattened top. The central marking cannot be as readily distinguished on all these specimens as it was on the Bonneterre material, but it is clearly visible on a few. This phenomenon may be caused by some specific variation or simply a matter of preservation.

The specimens are moderately abundant at the three horizons reported but have not been observed in any of the other collections.

Horizon and locality.—SM3, SM6, SM8

Figured specimens.—U.S.N.M. 138144—SM3; 138143—SM6.

Phylum BRACHIOPODA
Class INARTICULATA
Order ATREMATA
Superfamily-OBOLACEA
DICELLOMUS AMBLIA Bell,
Pl. 99, figs. 56–64

Dicellomus amblia Bell, 1944, in Lochman and Duncan, 1944, p. 149, pl. 18, figs. 23–31.

Remarks.—This species occurs in moderate abundance throughout the *Cedaria* zone in both sections. Over sixty valves which range in size from 0.25 mm. up to 5 mm. in length have been obtained. The larger valves are not common and may represent the largest adult size. The largest number and best preserved shells are from 1 to 3 mm. in size. In SM3, SM4 and SM7 a large number of embryonic shells have been recovered by etching with acetic acid. The abundance of small and medium-sized unbroken shells suggests that most of the material represents a biocoenose for this species. The embryonic valves may well have attached themselves to the trilobite exoskeletal debris on the sea bottom.

The interiors of some of the freed valves show the coarse punctae and muscle scars similar to those on valves figured by Bell.

Horizon and locality.—SM1, SM2, SM2a, SM3, SM4, SM7, OC3, OC4, 38-4, 40-34.

Figured specimens.—Broken valve, U.S.-N.M. 138179—OC3; valves, U.S.N.M. 138180a–e—OC4; large valve, U.S.N.M. 138182—SM1; valve, U.S.N.M. 138181—SM7; large valve, U.S.N.M. 138183—40-34.

DYSORISTUS LOCHMANAE Bell
Pl. 100, figs. 7–14

Dysoristus lochmanae Bell, 1944, in Lochman and Duncan, p. 147, pl. 18, figs. 32–37.
Dysoristus lochmanae Bell, Palmer, 1954, p. 766–767, Pl. 89, figs. 10,12,13.

Remarks.—A moderate number of valves belonging to this species were obtained from horizons in the upper part of the Middle *Cedaria* subzone in both sections. The species is clearly much less abundant than *Dicellomus amblia* with which it is associated at all these horizons. The stratigraphic range of *Dysoristus lochmanae* now appears to be definitely limited as the species also occurs in the Montana sections at essentially the same position. (23 valves in all)

Horizon and locality.—OC3, OC4, 40-34, SM1, SM2.

Figured specimens.—Valves, U.S.N.M. 138187a–c—SM2; valves, U.S.N.M. 138189a–d—OC4; valves, U.S.N.M. 138188a,b—40-34.

LINGULELLA MODESTA Lochman
Pl. 99, figs. 47–54

Lingulella modesta Lochman, 1940, p. 16–17, pl. 1, fig. 22.

Remarks.—This species is represented by a few small valves in the collections ranging through the lower 60 feet of the *Cedaria* zone in the Sheep Mountain section. The specimens are most abundant in SM7 and some valves reach a maximum length of 5 mm. The shell is quite thin and consequently most of the specimens, even in the etched residues, are fragmentary. A few of the valves have the outer surface well preserved so that they show the fine radiating costellae and the numerous concentric growth lines crossing the nacreous shell. None of the valves show well preserved interiors so that this portion of the shell is still unknown. The identification with the Missouri species has been made on the similarity in the thin shell structure, the symmetrical oval shape and the nature of the surface markings.

Horizon and locality.—SM3, SM4, SM7, SM8, SM8a, SM10.

Figured specimens.—Valve, U.S.N.M. 138176—SM4; valves, U.S.N.M. 138175a,b—SM3; valve, U.S.N.M. 138177—SM8a; valves, U.S.N.M. 138178a–d—SM7.

Order NEOTREMATA
Superfamily PATERINACEA
DICTYONINA sp.
Pl. 100, figs. 4–6

Remarks.—A few fragmentary valves showing the pitted surface ornamentation characteristic of *Dictyonina* occur only in two horizons near the top of the *Cedaria* zone in the sections. Several are figured for reference.

Horizon and locality.—SM1, OC4, 40-34.

Figured specimens.—Broken ventral valve, U.S.N.M. 138186—OC4; ventral valves, U.S.N.M. 138185a,b—SM1.

MICROMITRA MODESTA (Lochman)
Pl. 95, figs. 37–40

Paterina modesta Lochman, 1940, p. 14, pl. 1, figs. 20,21.
Micromitra modesta Lochman, Bell in Lochman and Duncan, 1944, p. 144, pl. 18, figs. 1–8,18, 19.

Remarks.—This species is represented by a small number of dorsal and ventral valves ranging from near the top to the lowest horizon of the *Cedaria* zone in the Sheep Mountain section, and also in one horizon in the Clear Creek section. Most of the specimens of adult size are broken but in SM7 there occur a number of immature unbroken valves. Some of the valves show the radiating "costellae" or flexures of the shell and some are without such a feature so that the species shows the same kinds of forms as are found in the Montana and Missouri faunas. The broken condition of the hinge line of the adult valves indicates that these shells were washed into the present sites from their places of attachment, which were probably not far distant.

Horizon and locality.—SM2, SM3, SM4, SM5, SM7, SM8, SM10, OC4, 40-34.

Figured specimens.—Broken ventral valve, U.S.N.M. 138213—SM2; dorsal and ventral valves, U.S.N.M. 138211—OC4; ventral valve, U.S.N.M. 138212—SM7; small dorsal, U.S.N.M. 138214—SM10.

Phylum MOLLUSCA
Class GASTROPODA
Family CYRTOLITIDAE
SEMICIRCULAREA ARCUATA Lochman
Pl. 99, figs. 33–46

Semicircularea arcuata Lochman in Lochman and Duncan, 1944, p. 81, pl. 12, figs. 22–27.

Remarks.—This species is well represented in both of the Wyoming sections. In the Sheep Mountain section it occurs in moderate numbers throughout the upper collections but becomes less common in the lowest horizons. At the Clear Creek locality it occurs in all the *Cedaria* zone collections and also in the basal *Crepicephalus* zone assemblage of OC2. The species appears to have a normal range through the *Cedaria* zone and into the *Crepicephalus* zone, but here as in Montana appears to reach its maximum abundance at the top of the middle *Cedaria* subzone. The Wyoming specimens range from shells under 1 mm. in length up to 4 mm. which is somewhat larger than any reported from Montana. Although many specimens are limestone steinkerns, there are many shells in which the outer surface with very fine growth lines paralleling the aperture is preserved. A few shells show these growth striae crossed by slightly coarser diagonal costellae, in a spiral pattern. A few of the steinkerns could be etched from the limestone by acetic acid in SM1—apparently they had been replaced by phosphatic material.

Horizon and locality.—OC3, OC4, SM1, SM2, SM3, SM5, SM6, SM7, SM8, SM8a, SM10, 40-34.

Figured specimens.—Shell, U.S.N.M. 138167—40–34; shells, U.S.N.M. 138169e,f,g,h—OC4; shell, U.S.N.M. 138166—SM1; shells, U.S.N.M. 138168c,d—SM2; shell, U.S.N.M. 138174—SM5; shell, U.S.N.M. 138170—SM6; shell, U.S.N.M. 138171—SM8; shell, U.S.N.M. 138172—SM8a; shell; U.S.N.M. 138173—SM10.

Incertae Sedis

HYOLITHES PRIMORDIALIS (Hall)

Pl. 98, figs. 60–69

Theca primordialis Hall, 1861, p. 48.
Hyolithes primordialis (Hall) Lochman, 1940, p. 23, pl. 2, figs. 8,9.

Remarks.—This species is represented by a moderate number of specimens from most of the collections in the Sheep Mountain section from SM2 down to SM10 and from OC3 in the Clear Creek section. Most of the specimens are limestone molds which only retain traces of the external shell. The specimens in OC3 represent adult shells which when whole measured approximately 18–20 mm. across at the aperture and 50 to 60 mm. in length. In shape the specimens show the characteristic flat surface on the side carrying the lip of the aperture, and a moderately arched dorsal side. The most complete specimens show that the shell was slightly curved from apex to aperture rather than being perfectly straight. One small, 2.5 mm. specimen of the original shell was etched from the limestone of collection SM8a with acetic acid. This specimen as well as those with patches of the outer surface reveal the details of surface ornamentation. Low clear-cut ridges cross the shell parallel to the aperture and occasionally bifurcate. On the small original shell they are spaced 6 or 7 in 0.25 mm. The wrinkles and depressions between them are crossed by very fine granular transverse striae or lines which are too fine to photograph. Several of the specimens show narrow longitudinal grooves running the length of the limestone mold. These are apparently features on the interior of the shell.

The specimens from the Sheep Mountain collections are predominately glauconitized, worn and decayed looking limestone molds of the interior. The abundance of this material suggests that most of these specimens were derived by the occasional settling of shells to a sea floor which was not normally receiving sediment. The material from SM6 is a good example. It contains over 20 glauconitized broken worn limestone molds of the interior, ranging in size from 5 mm. to pieces of very large shells, mixed with large and small glauconite grains. The few specimens with the shell preserved happened to be those which settled at the rare times that a current had spread organic debris over the bottom.

Two limestone molds of a flat circular object 6 mm. in diameter are covered with closely placed concentric wrinkles. The molds suggests that the original material was a semi-tough, flexible organic substance. They may represent the opercula of *Hyolithes*, though no specimens of *Hyolithes* were obtained from this horizon.

Horizon and locality.—OC3, SM2, SM3, SM4, SM5, SM6, SM8a, SM10, OC4, 40-34.

Figured specimens.—Molds of interior, U.S.N.M. 138147a,b—OC3; mold, U.S.N.M. 138148—SM3; decayed internal mold, U.S.N.M. 138149—SM4; mold and shell,

U.S.N.M. 138150— SM5; fragment with ventral lip, U.S.N.M. 138151—SM6; shell, and internal mold, U.S.N.M. 138152a,b—SM8a; mold, U.S.N.M. 138153—SM10; operculum, U.S.N.M. 138146—OC4.

Phylum ARTHROPODA
Class TRILOBITA
Order AGNOSTIDA
Superfamily AGNOSTACEA

BALTAGNOSTUS WYOMINGENSIS, n. sp.
Pl. 99, figs. 1–4

Cephalon subcircular, moderately convex, glabella conical, anterior lobe low, circular, posterior lobe rectangular, low in front, strongly convex in rear with one short pair of notches (lateral furrows) near front, a pair of small triangular basal lobes, dorsal and transverse furrows well defined, genae of medium width, moderately convex, border furrow broad, deep, border slightly convex, narrow.

Pygidium subcircular, convex, axial lobe more than twice width of pleural fields, convex anteriorly, sloping down steeply posteriorly, dorsal furrow narrow, distinct, anterior sides of axial lobe nearly straight, tapered only slightly to broad end of pseudolobe which does not touch the border furrow, two pairs of faint anterior axial furrows and elongate median node, terminal tubercle distinct, pleural fields steeply downsloping to broad border furrow, border narrow, slightly convex with a pair of small spines. Outer surface finely crinkled.

Remarks.—This form seems to be sufficiently different from *B. centerensis* Resser, the only species recognized by Palmer (1954) to merit description as a new species. Palmer states that *B. beltensis* Lochman is not recognized because the holotype pygidium is congeneric with *Kormagnostus*. This appears to be true. However, the paratype pygidium, smaller and broken, is very similar to the pygidia here described and the small cephalon (1 mm. in length) is definitely a *Baltagnostus* with the anterior lobe well defined. Palmer's assumption that the small cephalon could be an immature Kormagnostid is in error as the material from SM2 demonstrates that Kormagnostid cranidia 1.25 mm. in length show the obsolescence of the furrow around the anterior lobe. This feature must be considered a holaspid character which would appear in the 1 mm. instar.

DeLand and Shaw (1956) figure a cephalon and pygidium as *Kormagnostus* sp. indet. The cephalon, inspite of the poor figure, shows a well defined anterior lobe, while in the pygidium the axial lobe is narrower than that in *Kormagnostus* and the dorsal furrow essentially straight, so that there is no expansion of the pseudolobe, although DeLand and Shaw say "axial lobe expanding slightly on posterior half" (p. 557). Both cephalon and pygidium are best placed in *Baltagnostus*.

Horizon and locality.—SM2

Types.—Holotype, pygidium, U.S.N.M. 138154; paratypes, pygidium, U.S.N.M. 138155a; cephala, U.S.N.M. 138155b,c.

cf. BALTAGNOSTUS WYOMINGENSIS n. sp.
Pl. 99, fig. 32

One small, excellently preserved pygidium, 0.375 mm. in length, is tentatively referred to this species from horizon SM3, about 55 feet lower than SM2. The specimen is a meraspid but the distinct narrowing posteriorly of the pseudolobe suggests *Baltagnostus* rather than *Kormagnostus*. The distinctive crinkled or reticulate ornamentation of the outer surface is very well preserved.

Horizon and locality.—SM3.

Figured specimens.—Pygidium, U.S.N.M. 138164.

KORMAGNOSTUS SIMPLEX Resser
Pl. 99, figs. 5–31

Kormagnostus simplex Resser, 1938, p. 49, pl. 9, figs. 11–13.
Kormagnostus simplex Resser, Palmer, 1954, p. 718, pl. 76, figs. 8–12 (synonymy to date)

Remarks.—The species is represented in collections OC4 and OC3 by a moderate number of cephala and pygidia and it ranges through the Sheep Mountain section from SM1 down to SM8a, approximately 100 feet. Elsewhere the species is known to range throughout the *Cedaria* zone and into the base of the *Crepicephalus* zone. The authors accept Palmer's diagnosis of the species as a biospecies with a permissible amount of variation in form, especially in the pygidium, to include in the synonymy three other described species. The smallest cepha-

lon and pygidium obtained are 0.375 mm. in length from SM4, but at this size specific determination cannot be made, and the generic is uncertain. In the smaller pygidia (1 mm.) the sides of the pseudolobe tend to converge and the end does not quite reach the border furrow. However, one of the commonest variations is in the course of the accessory furrow, and one small pygidium from OC3 (pl. 99, fig. 30) actually shows a divergence of the furrow. Several of the pygidia are well enough preserved to show the terminal node of the axis. On small pygidia it appears right at the end of the pseudolobe but on the larger ones the inflation of the pseudolobe causes it to appear a short distance anterior to the end. Little variation is noted in the cranidium other than greater or less definition of the anterior lobe of the glabella, and some of this is certainly influenced by preservation since on peeled specimens an indication of very faint furrows around the anterior node can usually be seen.

The specimens range in size in the holaspid stage from 1 mm. up to 3 mm. in length. In SM6 there is an interesting mixture of fresh specimens and those which are well worn and appear to have been rolled or moved as if they were sand grains. The two types can be distinguished also by the fact that the worn material is composed of fine-grained, chocolate brown calcite of the same character as the associated limestone pebble and pellets while the fresh material is of very light gray, medium grained calcite.

The well preserved outer surface of the exoskeleton is covered with minute closely and irregularly arranged granules giving a crinkled appearance; the inner surface is apparently punctate.

Horizon and locality.—OC3, OC4, SM1, SM2, SM4, SM6, SM8, SM8a, 40-34, 39–51.

Figured specimens.—Cephalon, U.S.N.M. 138156f; pygidium, U.S.N.M. 138156a,e—OC3; cephala, U.S.N.M. 138163h,g,i; pygidia, U.S.N.M. 138163b,d,e—OC4; cephalon, U.S.N.M. 138159g; pygidium, U.S.N.M. 138159h—SM1; cephalon, U.S.N.M. 138160a; pygidia, U.S.N.M. 138160c,d,e,f—SM2; cephala, U.S.N.M. 138161e,f,d,g; pygidia, U.S.N.M. 138161h,i—SM6; cephalon, U.S.N.M. 138157a—SM8; pygidium, U.S.N.M. 138158c; SM8a; cephalon, U.S.N.M. 138162c; pygidia, U.S.N.M. 138162a, b—40-34.

cf. PROAGNOSTUS sp. undet.

A single immature cephalon, 0.375 mm. in length, has been tentatively identified as *Proagnostus.* The specimen is broken but appears to have had a glabella with both anterior and posterior lobes distinct and separated by a transglabellar furrow. In front of the broken glabella a median furrow can be seen clearly but the anterior border is broken also so the complete shape of the cephalon is not clear. *Proagnostus* is the only genus known in faunas of this age which has a median furrow in front of the glabella.

Horizon and locality.—SM4.

Family NORWOODIDAE
HOLCACEPHALUS TENERUS (Walcott)
Pl. 98, figs. 1–52

Norwoodia tenera Walcott, 1916, p. 172, pl. 28, figs. 2–2g.

Holcacephalus cf. *H. tenerus* (Walcott), Palmer, 1954. p. 742, pl. 84, fig. 3, (synonymy to date).

Remarks.—This species is another of the abundant, long-ranging (95 feet of the Sheep Mountain section) forms which were native to the region. In SM8 and SM5 it is represented only by adults, but at all the other horizons a large number of meraspids and a few protaspids can be associated with the adult forms. Approximately 150 specimens have been recovered. Most of the specimens must be molts as not a single librigena has been found. Two features of the cranidium which have been noticed in other areas as variations of the species, appear in the population of one horizon.

In the populations of SM8, SM6 and SM2 several holaspid cranidia show varying degrees of a posterior bending and sag. obsolescence of the anterior border furrow so that they approach in appearance *H. tenerus cuneiferus* from the Bonneterre of Missouri though none of the cranidia actually have a low median ridge on the preglabellar field as does the Missouri variety. They would, however, certainly appear to be individual variations in that direction.

In the population of SM2 several of the smaller cranidia show very well the pair of low nodes on the fixigenae opposite the base

of the glabella. Palmer (1954) calls attention to this feature on his seven Texas cranidia—the figured cranidium is 1.5 mm. in length but Palmer does not indicate how much of a size range exists. He also mentions the feature occurring on specimens studied by Rasetti (1946). His figured specimen (1.75 mm. in length) does not show the feature because of shadows in the dorsal furrow. In the Wyoming material the low nodes are a feature which is found on the latest meraspid cranidium (0.875 mm.) and on the early holaspid cranidia (up to 1.5 mm.) but cannot be distinguished on larger cranidia. This youthful feature in the western individuals of the species may have become established as a dominant characteristic in some of the other regions.

A number of the protaspids and meraspids have the paired antennary pits of the glabella very well preserved (pl. 98, figs. 9,11,12,47,48,50).

Horizon and locality.—SM2, SM3, SM4, SM5, SM6, SM7, SM8, SM8a.

EXPLANATION OF PLATE 97

FIGS. *1–8—Glaphyraspis occidentalis* Lochman. 1,4 dorsal of two normal cranidia, ×5.5, U.S.N.M. 137957d,c; *3,8*, dorsal, profile of undistorted cranidium with slightly longer glabella, ×5.5, U.S.N.M. 137957b; *2*, laterally crushed cranidium, ×5.5, U.S.N.M. 137957a; *6,7*, two broken pygidia, ×7.5, U.S.N.M. 137957f,e; *5*, associated librigena, ×5, U.S.N.M. 137957g, from OC1a.

9,10—Hypseloconus simplex Lochman. Anterior and side views of best steinkern, ×2, U.S.N.M. 137958, from OC1a.

11–13—Cheilocephalus sp. undet. *11*, mold of anterior fragment of a cranidium, ×2.2, U.S.N.M. 137959c; *12*, small, well preserved pygidium, ×2.2, U.S.N.M. 137959a; *13*, a larger, fragmentary pygidium, ×2.2, U.S.N.M. 137959b, from OC1a.

14—Uncaspis sp. undet. A single fragmentary pygidium, ×2.5, U.S.N.M. 137960, from OC1b.

15–20—Coosina ariston (Walcott). *15*, a fragmentary cranidium, ×3, U.S.N.M. 137961b; *16,17*, dorsal, profile of best cranidium, ×4. 6, U.S.N.M. 137961a; *18*, broken, immature pygidium with good outer surface, ×8, U.S.N.M. 137961c; *19,20*, profile, dorsal of large weathered pygidium, ×2, U.S.N.M. 137961d, from OC1b.

21–26—Tricrepicephalus cf. *T. coria* Walcott. *21*, anterior part of small cranidium, ×2.3, U.S.N.M. 137962a; *25*, mold of anterior part of larger cranidium, ×1.6, U.S.N.M. 137962b; *24,26*, large and small librigenae, ×1.3, ×2, U.S.N.M. 137962c,d; *22*, small pygidium with spines, ×3, U.S.N.M. 137962e; *23*, larger pygidium, spines broken, ×1.3, U.S.N.M. 137962f, from OC2.

27,28—Maryvillia sp. undet. Two small pygidia, ×3.4, ×3.7, U.S.N.M. 137963a,b, from OC2.

29–31—cf. *Coosina* sp. undet. *29,30*, profile, dorsal of largest pygidium, ×5, U.S.N.M. 137964a; *31*, small worn pygidium, same shape as fig. 18, ×8, U.S.N.M. 137964b, from OC2.

32—Lonchocephalus sp. undet. Single pygidium, ×7, U.S.N.M. 137965, from OC2.

33,34—Semicirculurea arcuata Lochman. Two of the larger steinkerns, 34 with some of the outer surface, ×4, U.S.N.M. 137966b,a, from OC2.

35,36—Genus and Species Undet. 3. Dorsal and profile of single pygidium, ×5.5, U.S.N.M. 137967, from 38–4.

37—Genus and Species Undet. 2. Dorsal of single pygidium, ×2.8, U.S.N.M. 137968, from SM10.

38,39—Genus and Species Undet. 1. Profile and dorsal of single cranidium, ×4.5, U.S.N.M. 137969, from OC3.

40,41—Billingsella sp. undet. Worn interiors of two ventral valves, ×4, U.S.N.M. 137970b,a, from OC2.

42–52—Minicephalus primus, n. gen., n. sp. *51*, holotype, broken cranidium with well preserved surface, ×3.2, U.S.N.M. 137971; *42,49,52*, paratype, mold from impression of fig. *52*, to show palpebral area, profile and dorsal of broken limestone mold, ×3.2, ×2.7, ×3.2, U.S.N.M. 137972a; *47,48*, paratype, profile, dorsal of small (1.5 mm.) cranidium, ×7, U.S.N.M. 137972d; *43*, paratype, associated librigena, ×3.2, U.S.N.M. 137972b; *45,50*, paratype, profile, dorsal of largest pygidium, ×2, U.S.N.M. 137972f; *46,44*, paratypes, two small pygidia, ×2, U.S.N.M. 137972e,g, from OC2.

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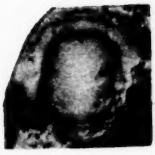
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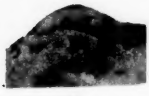
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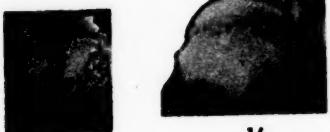
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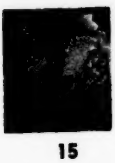
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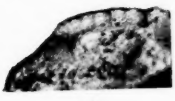
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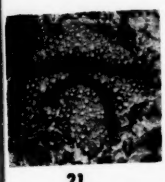
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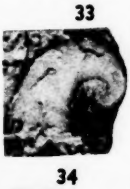
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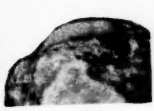
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Figured specimens.—Cranidia, U.S.N.M. 138141a–d; pygidia, U.S.N.M. 138141o,r; protaspids, U.S.N.M. 138141l,m,n; meraspids, U.S.N.M. 138141e,g,h,i,j,k—SM2; meraspids, U.S.N.M. 138140c–j—SM3; protaspid, U.S.N.M. 138139c; meraspids, U.S.N.M. 138139d,e,f,g,i; cranidia, U.S.N.M. 138139l,n,r; pygidium, U.S.N.M. 138139q—SM4; meraspid, U.S.N.M. 138138a; cranidia, U.S.N.M. 138138c,d—SM5; anaspid, U.S.N.M. 138137d; meraspids, U.S.N.M. 138137a–c; cranidia, U.S.N.M. 138137f,g; librigena, U.S.N.M. 138137h—SM6; protaspids, U.S.N.M. 138135a,b meraspids, U.S.N.M. 138135d,e,g; cranidium, U.S.N.M. 138135n; pygidium, U.S.N.M. 138135i,j—SM7; meraspid, U.S.N.M. 138136—SM8a.

Incertae Sedis
Genus and species undet. 1
Pl. 97, figs. 38,39

Cranidium subquadrate, moderately convex glabella with sides tapered to nearly straight front, two pairs of shallow lateral furrows, dorsal furrow deep at sides, shallow across front, occipital furrow distinct, occipital ring broken, frontal area just over 0.3 length of glabella with low median boss on preglabellar field, very faint, narrow anterior border furrow, anterior border a narrow downsloping rim; fixigenae convex, horizontal, palpebral area almost 0.66 of glabellar width, palpebral lobes under medium size and slightly anterior to glabellar center, posterior areas triangular, about same length

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EXPLANATION OF PLATE 98

FIGS. *1–52—Holcacephalus tenerus* (Walcott). *1,2*, adult cranidia showing variation in glabellar shape, ×9, U.S.N.M. 138138c,d; associated meraspid, ×26, U.S.N.M. 138138a, from SM5; *19*, early holaspid cranidium, ×13, U.S.N.M. 138141d; *4,5,18*, profile of 5,6, adult cranidia showing variation in width (sag) of preglabellar field and depth of anterior border furrow, ×9, U.S.N.M. 138141c,b,a; *16,17*, holaspid pygidia with posterior thoracic segment, ×26, U.S.N.M. 138141o,r; *7–12*, meraspid stages, *7*, ×20, rest ×26, U.S.N.M. 138141e,g,h,i,j,k; *13–15*, anaspid stages, in all note prominence of anterior pits, ×26, ×30, ×30, U.S.N.M. 138141l,m,n, from SM2. *20,21*, adult cranidia showing variation in glabella, ×9, U.S.N.M. 138137f,g; *22*, librigena, ×8, U.S.N.M. 138137h; *23*, associated anaspid, ×26, U.S.N.M. 138137d; *24–26*, associated meraspids, ×26, U.S.N.M. 138137a,b,c, from SM6, *27*, a late meraspid from SM8a, ×26, U.S.N.M. 138136. *28*, early holaspid cranidium, ×13, U.S.N.M. 138139l; *29,30*, adult cranidia, ×9, U.S.N.M. 138139n,r; *31*, latest meraspid pygidium with 2 thoracic segments, ×26, U.S.N.M. 138139q; *32–36*, associated meraspids, *32*, ×9, rest ×26. U.S.N.M. 138139i,g,f,e,d; *37*, anaspid, ×30, U.S.N.M. 138139c, all from SM4; *38–43*, series of meraspids, ×26, U.S.N.M. 138140c,d,e,f,g,h; *44,45*, late meraspid cranidia, note prominence of anterior pits and expanded anterior lobe of glabella, ×9, ×7, U.S.N.M. 138140i,j, all from SM3; *46*, holaspid pygidium with one thoracic segment, ×26, U.S.N.M. 138135i; *47*, smallest known anaspid, ×26, U.S.N.M. 138135a; *48*, slightly larger anaspid, ×30, U.S.N.M. 138135b; *49–51*, meraspids, ×20, ×15, ×26, U.S.N.M. 138135d,e,g; *52*, earliest holaspid cranidium, anterior lobe of glabella still slightly enlarged, ×9, U.S.N.M. 138135n, all from SM7.

53–55—Crinoidea A. *53*, calyx plate, ×2.6, U.S.N.M. 138142c; *54*, small modified plate, ×6, U.S.N.M. 138142a; *55*, radial plate, ×7.5, U.S.N.M. 138142b, all from SM2.

56—Dielymella? trituberculata, n. sp. Holotype, single valve, ×20, U.S.N.M. 138145, SM4.

57–59—Calcareous algae. *57,59*, side views of specimens from SM6, ×12, ×8, U.S.N.M. 138143a,b, *58*, top view of specimen from SM3, ×15, U.S.N.M. 138144.

60–69—Hyolithes primordialis (Hall). *60*, chitinous imprint, cf. operculum, ×5.3, U.S.N.M. 138146, from OC4. *61*, large fragment with outer surface ornamentation, ×2, U.S.N.M. 138152a; *63*, glauconitized internal mold, ×2.5, U.S.N.M. 138152b, from SM8a; *62*, small internal mold from SM5, ×4, U.S.N.M. 138150; *64*, side view of specimen from SM10, lowest horizon, ×3, U.S.N.M. 138153; *65*, worn internal mold from SM4, ×3.5, U.S.N.M. 138149; *66*, mold with perfect ventral lip, ×3.4, U.S.N.M. 138151, from SM6; *68*, characteristic medium-sized mold, ×1.8, U.S.N.M. 138148, from SM3; *67,69*, dorsal and ventral views of two large fragmentary specimens, ×0.8, ×1, U.S.N.M. 138147b,a, from OC3.

(tr) as occipital ring. Librigenae and pygidium not known. Outer surface covered with coarse granules.

A single fragmentary cranidium from horizon OC3 cannot be assigned to any known genus. In one or another feature the form resembles the cranidium of *Brassicicephalus* and of *Terranovella*, but the poor preservation and single specimen prevents a complete enough picture of this form to evaluate its generic relationships. Palmer (1954, pl. 87, fig. 10) shows a small cranidium from the *Crepicephalus* zone in Texas which may be related to this form.

Horizon and locality.—OC3.

Figured specimen.—Cranidium, U.S.-N.M. 137969.

Genus and species undet. 2
Pl. 97, fig. 37

A single well preserved medium-sized (5 mm. in length by 11 mm. wide) pygidium occurs in horizon SM10. Because of the small size of this collection it cannot be accurately associated with any cranidium, nor does it resemble any previously described form closely enough for generic identification. In the basic structure of the axis and the pleural regions the form resembles the pygidia of the related genera, *Talbotina* and *Weeksina;* but the axis is proportionately much wider and less tapered and in shape this pygidium is shorter and more transverse.

Horizon and locality.—SM10.

Figured specimen.—Pygidium, U.S.N.M. 137968.

Genus and species undet. 3
Pl. 97, figs. 35,36

A single pygidium 1.75 mm. in length was obtained from horizon 38-4. The specimen is a partially broken limestone mold and in structure resembles the pygidia associated with *Kingstonia* and *Bynumia*. However, it appears to differ in certain details from the described pygidia of these genera, and the collection is so small that no cranidia were obtained which could be associated with the form.

Horizon and locality.—38-4.

Figured specimen.—Pygidium, U.S.N.M. 137967.

Class Crustacea
Order Conchostraca
Dielymella? trituberculata, n. sp.
Pl. 98, fig. 56

The single specimen is an elongate-elliptical valve composed of several thin calcareo-phosphatic lamellae which retain a nacreous sheen. One side (interpreted as the hinge line) is perfectly straight, the other is continuously and smoothly curved and is edged by a narrow rolled (rim-like) margin. The anterior end is wider and rounder, while the other end (interpreted as the posterior) is narrower. Two large tubercles are located toward the anterior portion just below the hinge line, and a third tubercle is located at the same level on the posterior portion. The flaked condition of the lamellae over the limestone mold indicates that the outer surface of the shell is not preserved.

Remarks.—In shape the valve is most similar to those which have been assigned to *Dielymella*, a genus described largely from specimens in the early Middle Cambrian Bright Angel shale of the Grand Canyon section. But the presence and position of the three tubercles is quite unlike any Conchostraca described from the Cambrian. Most of the described North American forms are from Lower and early Middle Cambrian horizons. A few in northeastern Asia are known from highest Upper Cambrian or Tremadocian in age. This is the first specimen described from the Dresbachian anywhere in the world. The distinctive tubercle pattern certainly indicates a different species and the form may be found to represent a new genus when better material can be ottained.

Horizon and locality.—SM4.

Type.—Holotype, single valve: U.S.N.M. 138145.

Phylum Echinodermata
Crinoidea A
Pl. 98, figs. 53–55

Remarks.—A small number of plates showing the characteristic thick crystalline calcite texture of Echinodermata plates was obtained from SM2. Most of the plates are from 0.5 mm. to 1.5 mm. in diameter, a size range which appears to reflect the well sorted condition of the material at this horizon; but two fragments of larger plates,

measuring in their present condition 7 mm. in diameter were found. This is the maximum size of specimens in this horizon.

The specimens are referred to the Crinoidea rather than Cystoidea because the material shows a differentiation in shape among the plates as well as a variation in size. The two larger plates appear to have been hexagonal in outline and have had a single acentric boss as ornamentation. They probably represent the normal calyx plate. Several quite small plates are poorly hexagonal to circular in outline, with a low central ridge. A third type of plate appears to definitely be a radial plate (pl. 98, fig. 55) as one side is straight, thickened and crossed by two grooves which give the appearance of a primitive type of socket.

The material appears to represent a distinct species differing from that represented in SM6. It appears to be the same or a very closely related form to that found in the Nixon Gulch, Montana section, horizons 2.2 and 2.3, as the shape, size and the single prominent boss on each plate are much the same. From the associated trilobite species the material from the Nixon Gulch horizons and from SM2 appear to have occupied about the same ecologic conditions as well as the same time level.

Horizon and locality.—SM2, SM3, SM5.

Figured specimens.—Plates, U.S.N.M. 138142a,b,c—SM2.

Crinoidea B
Pl. 99, fig. 55

Remarks.—A single plate approximately 3 mm. in diameter appears to represent a second genus and species in the material from the lower horizon SM6. The surface of the plate is worn, but shows a distinctive pattern of a central boss with smaller rounded nodes around it, and a series of narrow ridges radiating in toward it but not touching it. The wear on the outer edges reveals a hollow in the ridges, suggesting that they mark the position of radiating canals of the water vascular system below the surface of the plate. This species is believed to represent the same form as that obtained from the lower *Cedaria* subzone in the Big Snowy and Little Belt Mountains of central Montana (Lochman and Duncan, 1944).

Additional broken plates were obtained from insoluble residues from three lower horizons.

Horizon and locality.—SM6, SM7, SM8, SM10.

Figured specimen.—Plate, U.S.N.M. 138165—SM6.

LATE MIDDLE CAMBRIAN FAUNA

Family Alokistocaridae
Mcnairia inornata Deiss
Pl. 100, figs. 39–40

Mcnairia inornata Deiss, 1939, p. 104, pl. 17, figs. 27–30.

Remarks.—A single cranidium from a very small collection seems to resemble Deiss' weathered holotype cranidium in essentially every detail. The palpebral lobes and posterior areas are somewhat better preserved on our specimen. Deiss made this species the genotype of the genus *Mcnairia*. The authors believe that this form may be found to be synonymous with *Parehmania* which was also described by Deiss in 1939. Deiss associated quite different pygidia with the cranidia of the two genera but the cranidia of the two genera are similar in many respects. Well preserved cranidia of *Mcnairia inornata* may show that the apparent differences have been caused by the poor preservation of the type material of *Mcnairia*.

Horizon and locality.—39–46.

Figured specimen.—Cranidium, U.S.N.M. 138193.

Family Dorypygidae
cf. Olenoides incertus Shaw
Pl. 100, fig. 41

Olenoides incertus Shaw, 1956b, p. 145, synonymy to date.

Remarks.—A single fragmentary cranidium is referred to this species which is based upon an *Olenoides* pygidium originally obtained by Miller in a collection 100 feet from the top of the Death Canyon in the South Fork of Teton Canyon Creek where it is associated with *Ithyektyphus tetonensis* (Miller). The pygidium in Miller's material designated the holotype by Shaw is Co. Univ. 12635.

Horizon and locality.—39–46.

Figured specimen.—Cranidium, U.S.N.M. 138194.

Family ANOMOCARIDAE
AMERICARE, n. gen.

Opisthoparian exoskeleton; cranidium rectangular, glabella narrow-elongate, low, front rounded, three pairs of shallow lateral furrows, frontal area more than one-third, but not quite one-half length (sag) of cranidium, with narrow convex preglabellar field, very broad concave anterior border furrow, and narrow slightly convex anterior border; fixigenae slightly upsloping, palpebral areas one-half glabellar width at middle, but narrow anteriorly, palpebral lobes long, arcuate with prominent palpebral rims and narrow deep furrows, situated just posterior center of glabella, narrow, short, slanted eye ridge, posterior area narrow, strap-like, same length (tr) as occipital ring. Librigena elongate-rectangular with broad concave lateral border furrow and nearly flat border, short genal spine. Pygidium semicircular, axis narrow, tapered 4/5th length, short postaxial ridge, 5 axial rings and long terminal, pleural field twice width of axis, slightly convex proximally changing to concave distally, no border furrow on exterior, 6 or 7 broad interpleural grooves, narrow shallow pleural furrows close to posterior edge of 1st, 2nd and 3rd segments. Outer surface covered with fine granules.

Genotype.—*Americare tetonensis* (Miller).

Remarks.—The pygidium and cranidium of this form are similar to those of *Glyphaspis* in many features and specimens of *Americare* recovered from the top of the Death Canyon member or the Park shales of the Gros Ventre have for several decades been referred to as "*Glyphaspis*" or *Glyphaspis*. The numerous specimens of cranidium and pygidium which have been obtained from SM21 indicate that the species is close to but certainly distinct from *Glyphaspis*, and actually may be more closely related to the European Anomocaridae in the manner in which the anterior branch of the facial suture runs abruptly in toward the glabella, leaving only a very narrow anterior portion to the palpebral area. *Glyphaspis capella* (Walcott), the genotype, and all other species of *Glyphaspis* described to date in which the cephalon is known have a much wider angle for the anterior branch of the facial suture. Both shale and limestone specimens are known so this feature cannot be attributed to preservation. The pygidium is very similar to that found in *Glyphaspis* and appears to differ only in the greater persistence of the narrow pleural furrows on the anterior segments. These are not evident on *Glyphaspis*.

Our knowledge of these late Middle Cambrian assemblages is not complete enough to determine whether the two genera have biostratigraphic significance. There is some indication at present that *Glyphaspis* is characteristic of the top of the *Bathyuriscus-Elrathina* zone and continues into the base of the overlying unnamed faunal zone, whereas *Americare* is common in and ranges through most of the unnamed faunal zone.

AMERICARE TETONENSIS (Resser)
Pl. 100, figs. 42–57

Glyphaspis cf. *G. perconcava* Poulsen, Miller, 1936b, p. 30, pl. 8, fig. 17.
Glyphaspis tetonensis Resser, 1937, p. 13.

Supplementary description.—Cranadium rectangular, glabella narrow-elongate, sides tapering gradually to rounded front, low convexity, three pairs of shallow lateral furrows, posterior two pairs diagonal, occipital furrow deep at sides, very shallow across center, occipital ring slightly convex, preglabellar field slightly convex, down-sloping, anterior border furrow one and one-half times width of preglabellar field, concave, anterior border narrow, slightly convex, rim-like; fixigenae very slightly upsloping, palpebral areas one-half glabellar width, narrowing markedly anteriorly, narrow, diagonal eye ridge, palpebral rim and furrow prominent, palpebral lobes more than medium-sized, situated somewhat posterior to the center of the glabella, posterior area narrow, same length (tr) as occipital ring. Librigena rectangular with broad lateral border furrow, flat lateral border and a short genal spine. Hypostoma narrow-ovate, convex oval anterior lobe, moderately convex semicircular posterior lobe, very narrow rim around posterior and sides, anterior border broken.

Pygidium semicircular, axis narrow, tapered 4/5th length to a narrow rounded end, short post-axial ridge, five axial rings and terminal, pleural field twice width of

axis, slightly convex proximally changing to concave distally, no border furrow on exterior, a very faint furrow sometime on interior just above the change of slope, 6, rarely 7, broad interpleural grooves, very narrow, shallow pleural furrows close to posterior edge of the first, second and sometimes the third segment. Outer surface closely covered with fine granules.

Remarks.—The type pygidium occurs in a black oolitic limestone 15 feet from the top of the Death Canyon member in the South Fork of Teton Canyon Creek section, and has a well preserved outer surface. The material in the Sheep Mountain section occurs as trilobite coquinal lenses in the lower 40 feet of the Park shale (upper Gros Ventre shales), and while the various parts of the exoskeleton are very abundant, nearly all are weathered internal molds, with only a few specimens retaining patches of the outer surface. The holotype pygidium clearly has seven interpleural grooves on the outer surface but no more than six can be distinguished on our specimens. It can not now be determined whether this feature is caused by preservation or is a biologic variation in the species. The two assemblages in which the form occurs do seem to be somewhat different since the holotype is associated with *Bolaspidella resseri* (Miller) at the type locality while the Sheep Mountain material occurs with the related *Josina festiva*.

Horizon and locality.—SM21.

Types.—Holotype, pygidium, Co. Univ. 12609; paratype, assoc. impression of cranidium, Co. Univ. 12609a; both from South Fork of Teton Canyon Creek, Teton County, Wyoming; plesiotypes, cranidia, U.S.N.M. 138192 a–e; plesiotype, librigena, U.S.N.M. 138192i; plesiotypes, pygidia, U.S.N.M. 138192f–h; plesiotype, hypostoma, U.S.N.M. 138192j—SM21.

Family MARJUMIIDAE
ITHYEKTYPHUS Shaw, 1956

This genus was established by Shaw for two species which had been described by B. M. Miller (1936b) from the upper part of the Death Canyon member and lower part of the overlying Park shale member of the Gros Ventre group in the northern Wind River Mountains and the Teton Range. *I. tetonensis* (Miller), the type species, occurs in the upper 100 feet of the Death Canyon member and was based on several imperfectly preserved cranidia. The second species, *I. tipparyensis* (Miller) occurred in the Park shales, 120 feet above the top of the Death Canyon.

Additional specimens of cranidia, and associated pygidia and librigenae of the type species have been obtained from a collection about 35 feet above the top of the Death Canyon cliff in the Sheep Mountain section. This material suggests the probability that *Ithyektyphus* is the immediate ancestor of *Modocia*, which occurs throughout the *Cedaria* zone in the same section. It is probable that cranidia of *Ithyektyphus* throughout the late Middle Cambrian beds in Montana and Wyoming have been assigned to *Modocia*. *Modocia nevadensis* Palmer from the lower part of the Hamburg limestone, Eureka district, Nevada, belongs to *Ithyektyphus*.

The cranidia of the two genera show many similarities but there are enough differences in the exoskeleton to warrant recognition of both genera especially since these morphologic differences clearly have biostratigraphic value. In the cranidium both genera have the same glabellar shape, broad at the base, then tapering rapidly to a narrow rounded front. But on *Modocia* the convexity of the glabella is low and the lateral furrows are essentially obsolete, while on *Ithyektyphus* the glabella is moderately convex and the lateral furrows, though weak, can still be distinguished. In all known species of *Ithyektypus* the preglabellar field is much narrower than the prominent convex anterior border. In *Modocia* there is a progressive widening (sag) of the preglabellar field while the anterior border remains prominent and convex. The palpebral lobes of both genera are the same size and in the same position, but the palpebral areas of *Ithyektyphus* are less than one-half the glabellar width while those of *Modocia* are at least two-thirds the glabellar width. In the librigenae the ocular platform of *Ithyektyphus* is consequently much wider than on the librigena of *Modocia*. The pygidia of the two genera show the same basic structure, but in *Ithyektyphus* there is at least one more segment and the marginal spines, though small, seem to be persistent in the adult.

Genotype.—Marjumia? tetonensis Miller, 1936, restricted.

ITHYEKTYPHUS TETONENSIS (Miller)

Marjumia? tetonensis Miller, 1936b, p. 129.
Ehmania tetonensis (Miller) Resser, 1937, p. 9.
Ithyektyphus tetonensis (Miller) Shaw, 1956b, p. 145.

Pl. 100, figs. 15–27

Supplementary description.—Cranidium quadrate, glabella broad-based, sides tapered rapidly to narrowly rounded front, three pairs of shallow, slanted lateral furrows, preglabellar field narrow (sag), horizontal, anterior border furrow broad, deep, anterior border twice width of preglabellar field, strongly convex, horizontal; fixigenae downsloping, palpebral areas less than one-half, more than one-third of glabellar width, palpebral lobes medium-sized, opposite center of glabella, eye ridge distinct, curved, posterior area of medium width, two-thirds length (tr) of occipital ring, with broad shallow border furrow. Librigena subquadrate, with broad, slightly convex ocular platform, narrow, only slightly convex, lateral border and flat medium-length genal spine. Pygidium subtriangular with wide, strongly convex axis, tapered only slightly to broad rounded end, nearly full length; four axial rings and terminal, pleural regions low, flat proximally, downsloping distally, same width as axis anteriorly, narrowing rapidly posteriorly, four segments with broad shallow pleural furrows, narrow faint interpleural grooves, no border furrow, no border except behind axis, five pairs of small pointed marginal spines.

Outer surface covered with medium to fine granules, with a pair of coarse granules on each axial ring of the pygidium.

Remarks.—The specimens in this collection have been referred to the type species. The type material is weathered external molds with a poorly preserved outer surface, though on two of the cranidia some medium-sized granules can be seen. The Sheep Mountain material consists of weathered peeled cranidia, librigenae and pygidia, except for two specimens on which the outer surface is preserved. The Sheep Mountain specimens appear to occupy approximately the same horizon in the Middle Cambrian section as the types.

The authors recognize three species belonging to *Ithyektyphus*. *I. tetonensis* is characterized by a low glabella, a horizontal, very narrow preglabellar field and a preglabellar field: border ratio of 1:2. *I. tipparyensis* has been examined and is recognized as a good species characterized by a slightly wider, downsloping preglabellar field, a preglabellar field: border ratio of 1:1.5 and a moderately convex glabella. *I. nevadensis* (Palmer) known from a single cranidium is also placed in this genus.

When Shaw (1956b) established this genus, he indicated (p. 145) under his discussion of the type species—that the cotypes were Co. Univ. 12607. However, examination of the Miller types shows that only one cranidium, that on pl. 8, fig. 19 (Miller, 1936b) carries the number 12607. This is a weathered limestone mold and must be considered the Holotype. The other piece in this lot carries the number 12610 and consists of a small slab of limestone on which there are several weathered cranidia and two impressions of cranidia, all belonging also to *Ithyektyphus tetonensis*. A plasticine mold of the largest impression is still in the box. It also is numbered 12610 and is Miller's fig. 20. This cranidium must be considered a paratype. Miller had originally associated with these cranidia, an *Olenoides* pygidium which he figured on pl. 8, fig. 21. To this pygidium Shaw gave the new name —*Olenoides incertus* Shaw—but mistakenly indicated this specimen as Co. Univ. 12610. Evidently Shaw did not see the specimen as it bears the number—Co. Univ. 12635.

Horizon and locality.—SM21.

Plesiotypes.—Cranidia, U.S.N.M. 138184a–d; librigenae, U.S.N.M. 138184g; pygidia, U.S.N.M. 138184e,f.

Family MENOMONIIDAE
JOSINA, n. gen.

Opisthoparian exoskeleton, cranidium with elongate glabella tapered to narrow rounded front, three pairs of deep short lateral furrows, preglabellar field narrow (sag), widening exsag., anterior border furrow curved, convex anterior border; fixigenae upsloping, palpebral area same width as glabella at midwidth, palpebral lobes medium size, opposite anterior third of glabella, eye ridge narrow, longer (tr) than occipital ring. Outer

surface densely granular. Librigena, thorax and pygidium not known.

Genotype.—Josina festiva, n. gen., n. sp.

JOSINA FESTIVA, n. sp.
Pl. 100, figs. 28–35

Cranidium quadrate, glabella elongate with sides tapered to narrowly rounded front, three pairs of short deep lateral furrows, anterior pair straight, posterior pairs diagonal, occipital furrow deep and wide at sides, shallow across center, occipital ring of medium width, flat, preglabellar field downsloping, narrow on sag. line, widening at sides, shallow, posteriorly curved anterior border furrow, narrow convex border, widest on sag. line; fixigenae upsloping, palpebral areas same width as glabella, palpebral lobes opposite anterior one-third of glabella, palpebral rim prominent, narrow palpebral furrow, eye ridge narrow, straight, posterior area one and one-third length (tr) of occipital ring, narrow, with broad shallow posterior furrow. Outer surface densely covered with medium-sized granules. Librigena, thorax and pygidium not known.

Remarks.—Seven cranidia, all about the same size, from 2 to 2.5 mm. in length, represent this new form.

This genus and species appears to be another member of the Menomoniidae and may be the common ancestor of several of the Dresbachian genera. The structure of the cranidium, the only part known, shows affinities with both *Densonella* and *Bolaspidella*. The fixigenae are not as wide as in *Bolaspidella* nor as narrow as in *Densonella* but they are slightly upsloping (about 15°)as in the primitive *Densonella* species. The backward curvature of the anterior border furrow and the sagittal thickening of the border resembles the condition found in both *Densonella* and *Menomonia*. The medium-sized palpebral lobes and eyes, with prominent palpebral rims, are characteristic of the entire family; and their anterior position is the same as in *Densonella praesemele*.

The species is considered a new generic type because it differs noticeably from all other members of the family in the narrow elongate shape of the glabella with the three pairs of lateral furrows widely spaced along it. In the other genera the glabella is short, subquadrate to subtriangular in shape, with the short triangular shape becoming more pronounced as the elevation of the fixigenae increases.

Horizon and locality.—SM21.

Types.—Holotype, cranidium, U.S.N.M. 138190; paratypes, cranidia, U.S.N.M. 138191a–e.

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EXPLANATION OF PLATE 99

FIGS. *1–4—Baltagnostus wyomingensis*, n. sp. *1*, paratype, large, well preserved cephalon, ×5, U.S.N.M. 138155b; *2*, paratype, weathered cephalon, ×6, U.S.N.M. 138155c; *3*, holotype, pygidium with outer surface, ×7.3, U.S.N.M. 138154; *4*, paratype, small pygidium showing end of axial lobe, ×16, U.S.N.M. 138155a, from SM2.

5–31—Kormagnostus simplex Resser. *6,5,8*, series of three pygidia showing broadening of pseudolobe with increase in size, ×8, ×8, ×5.2, U.S.N.M. 138163b,e,d; *9,10*, unpeeled cephalon showing two pairs of lateral furrows on posterior glabellar lobe, ×9, U.S.N.M. 138163h,g; *7*, large unpeeled cephalon, ×5.2, U.S.N.M. 138163i, all from OC4; *11,12*, unpeeled and peeled adult pygidia, ×5.2, ×7, U.S.N.M. 138161h,i; *13,16*, peeled and unpeeled cephala not water worn, ×6, ×9, U.S.N.M. 138161d,e; *14,15*, cephala showing abrasion, ×9, ×6, U.S.N.M. 138161g,f, all from SM6; *17,18,19*, peeled cephalon and associated well-preserved pygidia, ×6, ×6, ×9, U.S.N.M. 138162c,b,a, from 40–34; *22*, peeled cephalon, ×8, U.S.N.M. 138160a; *26,23,21,20*, series of pygidia showing change in length and breadth of axis with growth, ×9, ×5.2, ×8, ×6, U.S.N.M. 138160c,d,e,f, from SM2; *24,25*, pygidium and cephalon from SM1, ×9, ×8, U.S.N.M. 138159h,g, from SM1; *27*, small pygidium from SM8a, ×9, U.S.N.M. 138158c; *28*, well-preserved cephalon from SM8, ×9, U.S.N.M. 138157a; *30*, small pygidium with distinct axial node, ×10, U.S.N.M. 138156a; *29,31*, fragmentary adult cephalon and pygidium, ×9, ×5, U.S.N.M. 138156f,e, from OC3.

32—Baltagnostus cf. *B. wyomingensis*, n. sp. Immature pygidium, ×10, U.S.N.M. 138164, from SM3.

33–46—Semicirculatea arcuata Lochman. *33*, shell showing growth lines, ×5, U.S.N.M. 138166, from SM1; *34*, shell from 40–34 with median ridge, ×8, U.S.N.M. 138167. *35,36,41*, apertural view of *36*, two steinkerns from SM2, ×8,×9, U.S.N.M. 138168d,c. *39,45*, shells showing growth lines and median ridge, ×6, ×8, U.S.N.M. 138169e,f; *38*, view of freed shell showing torsion of apex, ×8, U.S.N.M. 138169g; *40*, shell with transverse lirae, ×7, U.S.N.M. 138169h, all from OC4; *42*, steinkern from SM5, ×8, U.S.N.M. 138174; *46*, shell from SM6 with growth lines and transverse lirae, ×9, U.S.N.M. 138170; *43,44*, small shells from SM8, and SM8a, ×6, ×8, U.S.N.M. 138171, 138172; *37*, small shell from SM10, lowest horizon, ×11, U.S.N.M. 138173.

47–54—Lingulella modesta Lochman. *49,51*, well-preserved brachial valves, ×5, ×8, U.S.N.M. 138175b,a, from SM3; *48*, pedicle valve from SM4, ×14, U.S.N.M. 138176; *47,52*, fragments of pedicle valves showing radiating costellae, ×4.5, U.S.N.M. 138178b,c; *50*, brachial valve with growth lines, ×20, U.S.N.M. 138178a; *53*, interior of pedicle valve, ×4.5, U.S.N.M. 138178d, all from SM7; *54*, brachial valve from SM8a, ×5, U.S.N.M. 138177.

55—Crinoidea B. Ornamented calyx plate, ×8, U.S.N.M. 138165, from SM6.

56–64—Dicellomus amblia Bell. *57*, broken valve from OC3, ×6, U.S.N.M. 138179; *56*, brachial view of specimen with both valves, ×10, U.S.N.M. 138180a; *58–61*, four valves of varying sizes, ×4.2, ×4, ×10, ×6, U.S.N.M. 138180b,c,d,e, all from OC4; *62*, pedicle valve from SM7, ×6.4, U.S.N.M. 138181; *63*, large, partially peeled valve from SM1, ×3.4, U.S.N.M. 138182; *64*, large broken valve from 40–34, ×5, U.S.N.M. 138183.

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U. S. Geol. Survey Prelim. Map 31.

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EXPLANATION OF PLATE 100

FIGS. *1–3*—*Ithyektyphus tipperaryensis* (Miller). Dorsal, profile and front views of holotype cranidium, only known specimen, ×2.2, Co. Univ. 12606, Crow Creek Canyon, 3 miles north of Tipperary, Fremont Co., Wyoming.

4–6—*Dictyonina* sp. *4,5*, fragmentary valves from SM1, ×7, ×5, U.S.N.M. 138185b,a; *6*, broken valve from OC4, ×5, U.S.N.M. 138186.

7–14—*Dysoristus lochmanae* Bell. *10,11*, valves from SM2, ×10, ×6, U.S.N.M. 138187a,c; *9,14*, a small peeled valve and a larger valve from 40–34, ×10, U.S.N.M. 138188b,a; *7,8,12,13*, series of four valves from OC4, ×8, ×6, ×6, ×10, U.S.N.M. 138189b,a,c,d.

15–27—*Ithyektyphus tetonensis* (Miller). *15,16,17*, dorsal, front and profile of holotype cranidium, ×1.3, Co. Univ. 12607, South Fork of Teton Canyon Creek, Teton Co., Wyoming; *18,23,24*, dorsal, profile and front of small peeled but complete plesiotype cranidium, ×5.8, ×5, ×5, U.S.N.M. 138184d; *22,27*, larger peeled plesiotype cranidia, showing fine granules and lateral furrows, ×2.6, ×3.5, U.S.N.M. 138184b,c; *25*, largest plesiotype cranidium, ×2, U.S.N.M. 138184a; *26*, plesiotype librigena with some outer surface, ×1.5, U.S.N.M. 138184g; *21,20*, dorsal and profile of large plesiotype pygidium, ×1.6, U.S.N.M. 138184f; *19*, small plesiotype pygidium with worn outer surface, ×3.7, U.S.N.M. 138184e, all from SM21.

28–35—*Josina festiva*, n. gen., n. sp. *32,35*, holotype, dorsal and front of cranidium with outer surface, ×6, U.S.N.M. 138190; *31,34*, paratype, profile and dorsal of cranidium with posterior area, ×6, U.S.N.M. 138191a; *33*, paratype cranidium with right posterior area, ×6, U.S.N.M. 138191e; *28–30*, paratype cranidia, ×6, U.S.N.M. 138191d,c,b, all from SM21.

36–38—*Bolaspidella resseri* (Miller). Profile, front and dorsal of holotype cranidium, a weathered limestone mold, ×3.7, Co. Univ. 12608, South Fork of Teton Canyon Creek, Teton Co., Wyoming. This cranidium appears in the upper right hand corner of Miller's pl. 8, fig. 39. The rest of the block shown by Miller had by 1958 been broken away from the specimen.

39–40—*Mcnairia inornata* Deiss. Dorsal and profile of single small cranidium, ×3, U.S.N.M. 138193, from 39–46.

41—cf. *Olenoides incertus* Shaw. Single fragmentary cranidium, ×1, U.S.N.M. 138194, from 39–46.

42–57—*Americare tetonensis* (Resser), n. gen. *56,50*, dorsal and profile of holotype pygidium, ×1.5, Co. Univ. 12609; *54,46*, dorsal and profile of paratype cranidium, rubber mold of an impression on same piece with holotype, ×1.5, Co. Univ. 12609a, South Fork of Teton Canyon Creek, Teton Co., Wyoming; *45,55*, dorsal and profile of plesiotype, most complete cranidium, ×2.3, U.S.N.M. 138192a; *44*, plesiotype cranidium with some outer surface, ×2, U.S.N.M. 138192b; *43,47,49*, plesiotype cranidia, ×4, ×2, ×2.6, U.S.N.M. 138192d,c,e; *42*, plesiotype, associated hypostoma, ×2.2, U.S.N.M. 138192j; *52*, plesiotype, associated librigena, U.S.N.M. 138192i; *48,53*, plesiotypes, medium-sized and large pygidia, ×1.5, ×1.3, U.S.N.M. 138192h,f; *51,52*, plesiotype, profile and dorsal of small pygidium, ×1.5, U.S.N.M. 138192g, all from SM21.

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JOURNAL OF PALEONTOLOGY, V. 34, NO. 5, P. 835–858, PLS. 101–107, 2 TEXT-FIGS., SEPTEMBER, 1960

MOLLUSCA OF THE CRETACEOUS BALD HILLS FORMATION OF CALIFORNIA

PART I

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ABSTRACT—A well preserved molluscan fauna has been collected from previously undescribed Cretaceous rocks in the northwestern Sacramento Valley, California. The fossils occur in the Bald Hills formation, a 1000-foot to 1900-foot thick southeast dipping conglomerate, graywacke, and mudstone unit which ranges in age from Late Albian to Late Cenomanian. The gastropod and cephalopod elements of this fauna number thirty-two species, seventeen of which are new.

New species described are: *Solariella stewarti, Tessarolax trinalis, Gyrodes allisoni, Gyrodes greeni, Ampullina stantoni, Ampullina mona, Euspira popenoei, Euspira marianus, Paleosephaea sacramentica, Clinura anassa, Acteon sullivanae, Cylichia andersoni, Mariella (Mariella) fricki, Turrilites (Turrilites) dilleri, Puzosia puma, Puzosia sullivanae, Eogunnarites matsumotoi.*

INTRODUCTION

A LARGE number of well preserved Cretaceous mollusks has been collected from previously undescribed rocks in the northwestern Sacramento Valley, Shasta County, California. This paper describes and discusses the cephalopod and gastropod elements of this fauna and defines the Bald Hills formation, the unit in which they occur.

The writers wish to acknowledge the comments and suggestions of Ralph Imlay, Davis Jones, Tatsuro Matsumoto and Willis Popenoe concerning the systematic part of this paper, and the financial assistance of the Humble Oil and Refining Company, the University of California, Riverside Intramural Research Fund and the National Science Foundation during the field investigations.

THE BALD HILLS FORMATION

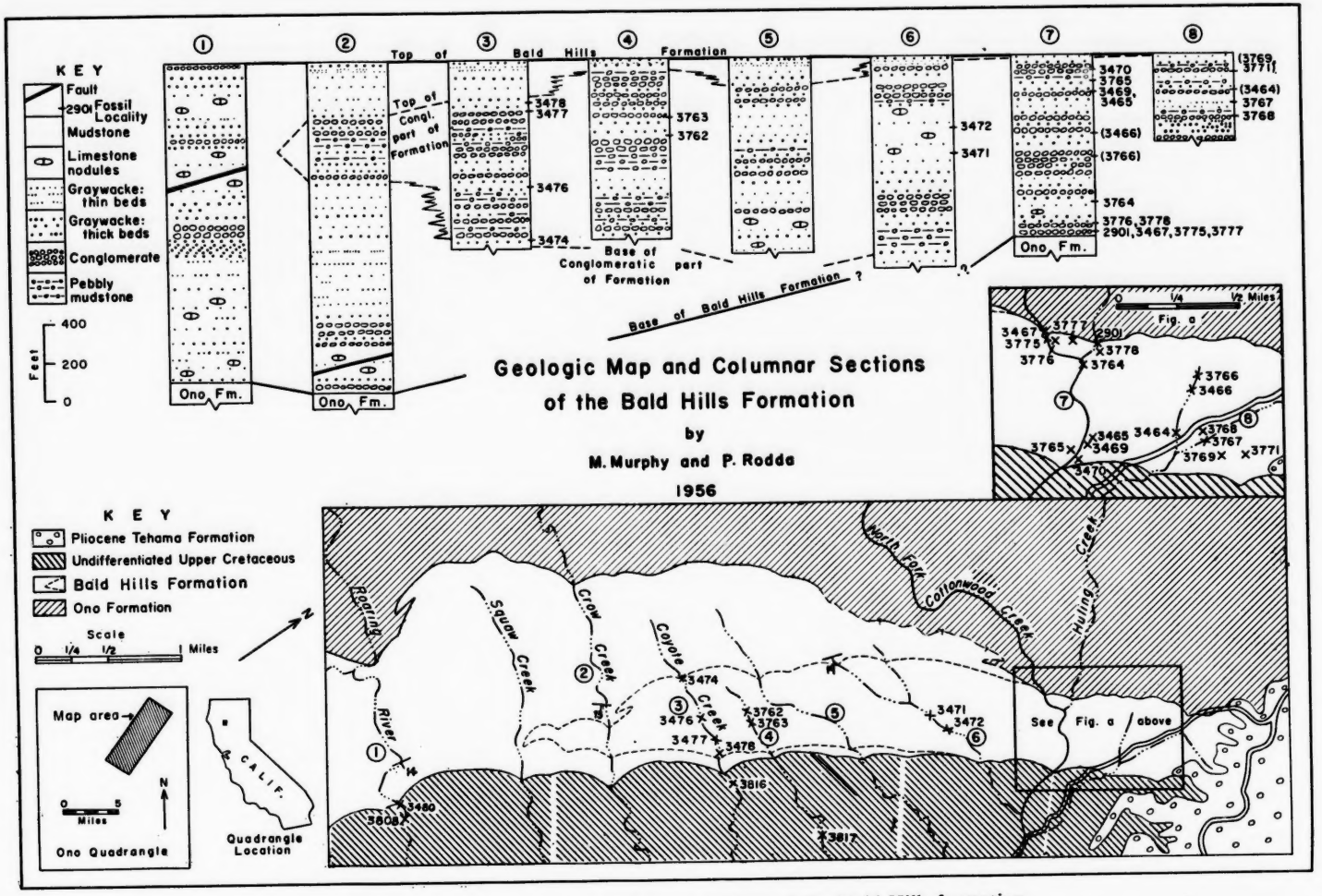
The Bald Hills formation is a conglomerate, sandstone and mudstone unit cropping out in the northeast quarter of the Ono Quadrangle (see index map). It rests comformably on the dark gray mudstone of the Ono formation (Murphy, 1956, p. 2105–2111) and is overlain conformably by an as yet unnamed Upper Cretaceous mudstone unit. The formation as presently recognized has been traced from the Igo-Cottonwood road south-southwest to Roaring River and supports the relatively high ridges of the Bald Hills from which it derives its name. The conglomerate units in this part of the section on Dry Creek in Tehama County probably should be included in the formation but detailed mapping in that area is not yet complete.

In the area adjacent to the North Fork of Cottonwood Creek the base of the formation is marked by a fossiliferous bed of cobble conglomerate about 10 feet thick. This conglomerate or a similar unit is exposed at the base of the formation at outcrops between the North Fork and Crow Creek. The base of the formation farther south on Roaring River is marked by a thick bed of graywacke.

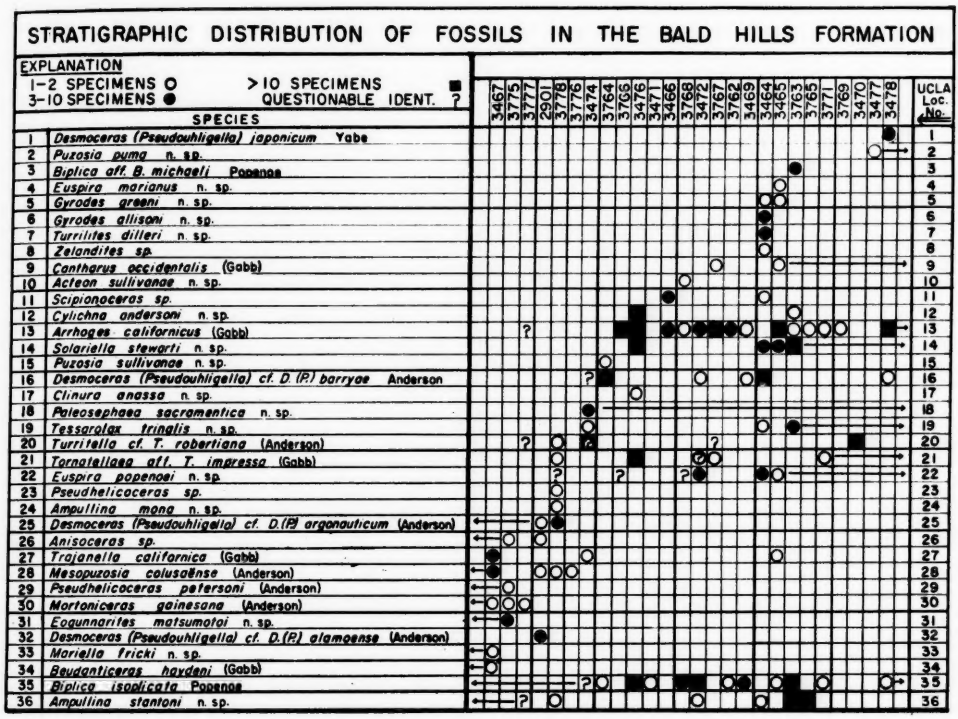
The top of the Bald Hills formation is usually marked by a sequence of closely spaced, thin graywacke beds (see columnar sections 2 to 6, plate 1) followed by one or two thick graywacke beds which, in turn, are overlain by the mudstone of the overlying formation. On the North Fork of Cottonwood Creek the contact is gradational between coarse-grained sandstone and conglomerate and the mudstone of the overlying formation.

At the northeastern end of its outcrop area the Bald Hills formation contains many conglomerate beds distributed throughout

[1] Cost of two plates borne by National Science Foundation.



TEXT-FIG. 1—Geologic map and columnar sections of the Bald Hills formation.



TEXT-FIG. 2—Stratigraphic distribution of gastropods and pelecypods in the Bald Hills formation. Arrows indicate that the species has also been found above, or below, the Bald Hills formation.

the section. Some of these beds have been traced for strike distances of half a mile before pinching out or being lost under a soil and vegetation cover. As the formation is traced southward the highly conglomeratic portion of the section becomes restricted to the upper part of the formation and fewer conglomerate beds are present. This part of the formation is outlined on the map by a somewhat arbitrarily place dashed line.

Other conglomerates are exposed in the lower part of the formation on Roaring River and Crow Creek. On Crow Creek a small lens about 150 feet thick occurs about 300 feet above the base of the formation. A strongly conglomerate section about 75 feet thick occurs about 700 feet above the base of the formation on Roaring River. This conglomerate is apparently the northern extension of a conglomerate unit that extends at least as far south as the Middle Fork of Cottonwood Creek. Its northern limit is the first small valley north of Roaring River.

The conglomerates of the Bald Hills formation are similar throughout. The grain size ranges from fine sand to boulders with the average cobble about 2 inches in diameter. The clasts are usually well rounded and set in a matrix of medium- to coarse-grained graywacke or very sandy mudstone. The majority of the cobbles are dark colored porphyritic volcanic rocks. The remainder includes metamorphic and granitic rocks, cherts, and mudstone and limestone clasts. The conglomerates are sometimes fairly well bedded, especially near their tops. The bases of the conglomerate units are usually irregular, perhaps as a result of channeling or other disturbances of the underlying sedimentary rocks which are predominantly mudstones. At their tops the conglomerate beds almost always grade upward to massive, then finely bedded sandstone.

The type section of the Bald Hills formation is in the Bald Hills along Crow Creek in sections 25, 26, and 31, T. 30 N., R. 7 W.,

TEXT-FIG. 1—Geologic map and columnar sections of the Bald Hills formation.

Mount Diablo Base and Meridian. The type section was chosen here because it is almost continuously exposed from base to top and shows a more or less usual sequence of rock types for this stratigraphic interval in the Ono Quadrangle.

LITHOLOGY OF THE TYPE SECTION

350′	graywacke and mudstone—alternating sequence in which the thickness of the graywacke beds gradually diminishes from bottom to top, averaging 3′ per bed in the lower part of the unit, 1′ per bed in the middle part of the unit and 6 inches per bed in the upper part of the unit. At the top of the sequence is a graywacke bed two feet thick. This unit marks the top of the Bald Hills formation.
10′	conglomerate and graywacke
180′	mudstone and graywacke (60%) alternating with pebbly mudstone (40%).
50′	graywacke and mudstone—as below
6′	pebbly mudstone—scattered cobbles averaging two inches in diameter in a matrix of sandy mudstone.
50′	graywacke and mudstone—as below.
2′	conglomerate
370′	graywacke (60%) and mudstone (40%) —as below; graywackes range in thickness from 4 inches to 1 foot.
500′	mudstone—massive, dark gray mudstone with a few thin, flaggy graywacke beds intercalated
150′	conglomerate—cobble conglomerate lentil that lenses out rapidly in both directions in the outcrop.
200′	graywacke and mudstone—medium—to coarse-grained graywacke beds ranging in thickness from a few inches to about two feet interbedded with approximately equal thicknesses of finer grained graywacke and mudstone; the graywacke beds are very well indurated and rarely contain fossils.
2′	conglomerate, fossiliferous, average cobble size about 2 inches
1870′	Total

THE AGE OF THE BALD HILLS FORMATION

The Bald Hills formation ranges in age from upper Albian through Cenomanian and possibly into the lower Turonian.

The oldest definitely dated bed is the nodular mudstone lying next above the lowest conglomerate on Huling Creek. This unit has yielded specimens of *Pseudhelicoceras*, *Desmoceras* (*Pseudouhligella*) and *Mesopuzosia*. This assemblage places it in the upper Albian even though this position is far below the reported range of *Mesopuzosia*.

The top of the formation in the area adjacent to the North Fork of Cottonwood Creek is below the last occurrence of *Eogunnarites* and *Desmoceras* (*Pseudouhligella*) and, therefore, is probably of Cenomanian age. The top of the formation on Roaring River is just a few feet below U.C.L.A. Locality 3808 which has yielded a specimen of *Gaudryceras* cf. *G. densiplicatum* (Jimbo), a form not found below the Turonian in Japan.

The lowest unit of the formation on the North Fork of Cottonwood Creek and on Huling Creek is a very fossiliferous cobble conglomerate from which the majority of the ammonite specimens collected in the formation have come. On the North Fork this unit consists of a lower 2–3 feet of conglomerate with a sandy matrix. This grades upward into a typical "pebbly" mudstone about three to four feet thick. The upper four feet of the unit consists of cobble conglomerate in a mud and sand matrix. The clasts are largely of limestone derived from the underlying formation or from deposits accumulating penecontemporaneously in other areas. It is in the limestone nodules that the bulk of the well-preserved fossils occurs. It is impossible in many cases to tell whether these nodules are indigenous or derived from another source but in many instances it is clear that they are clasts in the conglomerate. The evidence for reworking is as follows:

(1) the presence of ammonites otherwise only known from the Aptian or Barremian parts of the section in the nodules e.g. *Phylloceras* sp. (an Aptian form) and *Shasticrioceras* sp. (a Barremian form);
(2) hemispherical nodules with the edges of the flat side angular because of breaking during transportation;
(3) blocks of *Cucullaea truncata*-bearing sandstone in a muddy sandstone or mudstone matrix of different grain size, color and texture;
(4) all fossils found in the matrix are broken and weathered and show evidence of transportation, whereas the fossils in the nodules are excellently preserved and most are different species;
(5) no evidence that fossils only partially enclosed in nodules were ever present in the adjacent matrix;
(6) the nodules are oriented in the conglomerate against other clasts as would be expected for clasts, i.e., they touch but never

fit around other clasts; they have shell debris plastered on the outside but never incorporated in the nodule; they are arranged with their long dimensions at various angles to the bedding, a condition not yet encountered in the nodular mudstones in other parts of the section.

From the above listed data it is inferred that most, if not all, the forms occurring in nodular limestone in the conglomerate are reworked. The age of this bed is upper Albian. This age assignment is based on the stratigraphic position of the bed between the upper Albian bed bearing *Pseudhelicoceras* which lies immediately above, and the upper Albian beds below bearing *Mortoniceras*, *Desmoceras* (*Pseudouhligella*), and *Zelandites*.

Some of the species found in the nodules and other reworked sedimentary rocks were extant at the time this conglomerate unit was deposited. For example, *Mesopuzosia colusaense* (Anderson) occurs free in the matrix, in nodular limestone clasts in the conglomerate, and in the nodular mudstone above the unit; *Cucullaea truncata* Gabb occurs below, above and in the matrix of the conglomerate as well as in the clasts in the conglomerate.

Many of the fossils found in clasts in the conglomerate are also upper Albian in age. This age is certain as the lowest occurrence of many of the genera in the clasts is upper Albian, e.g. *Eogunnarites*, *Mariella*, *Desmoceras* (*Pseudouhligella*), and *Anisoceras*. Beds with *Pseudhelicoceras*, whose range is middle and upper Albian, lie immediately above the conglomerate.

These facts show that during the upper Albian active uplift and erosion of Cretaceous sediments ranging in age from at least Barremian to Albian was taking place in northern California, probably in areas not too distant from the present outcrop of this unit. The direction of these localities is as yet unknown.

SYSTEMATIC DESCRIPTIONS

Class GASTROPODA

Family TROCHIDAE

Genus SOLARIELLA Wood 1842

SOLLARIELLA STEWARTI n. sp.

Pl. 103, figs. 4,5

Shell small, low spired, turbinate, spire about one half the height of the shell; whorls number about 5; shell covered by numerous spiral lines which are most prominent in the umbilicus and on the shoulder and faintest, sometimes nearly absent, at the middle of the whorl; lines of growth slant well forward from just above the umbilical edge to the posterior margin of the whorl; distinct rib-like crenulations are present on the shoulder and umbilical angle; the crenulations are prominent and about 45 in number on the penultimate whorl but poorly developed on the last whorl; aperture sub-circular, acute posteriorly; umbilicus perspective, deep.

Types.—The holotype and paratype are numbers 28622 and 28623, respectively, in the U.C.L.A. Invert. Paleo. Catalogue. Dimensions: height 8 (7) mm., height of spire 4 ($3\frac{1}{2}$) mm., maximum width of shell 10 ($7\frac{1}{2}$) mm., respectively.

Remarks.—The species is found in abundance at localities 3476 and 3763 in the upper part of the Bald Hills formation. It also occurs in the overlying formation.

S. stewarti somewhat resembles published figures of *S. angulata* (Gabb) (Gabb, 1869, pl. 28, fig. 55; Stewart, 1926, pl. 24, fig. 17), but adequate comparisons are difficult to make. *S. angulata* appears to have a higher spire, a more gently sloping posterior flank, and an angulate whorl profile. The type lot of *S. angulata* has been examined, but the lectotype was not present, and is presumably lost. None of the other specimens in the type lot appears to be conspecific with *S. angulata*, but two other species are represented, one of which is *S. stewarti* n. sp. The other species is undescribed. Gabb reported *S. angulata* only from Martinez.

This species is named for Ralph Stewart.

Family PSEUDOMELANIIDAE

Genus TRAJANELLA Popovici-Hatzeg, 1899

TRAJANELLA CALIFORNICA (Gabb)

Pl. 101, fig. 30

Acteonina californica Gabb, 1864, p. 114, pl. 19, fig. 68; Stewart, 1926, p. 433, pl. 24, fig. 21; Anderson, 1958, p. 156, pl. 29, fig. 1.

Shell large, thick, elongate conoid; spire about one half the height of shell; whorls high and number about 7; ornamented only by sinous lines of growth that are usually faint but sometimes incised and prominent; whorls shallowly and evenly convex; suture shallowly impressed; inner lip and part of

the base of aperture covered by moderate to heavy callus.

Type specimen.—Stewart (1926, p. 433, pl. 24, fig. 21) studied Gabb's original material but did not select a lectotype. According to Stewart two lots of the type material exist. The material at the Academy of Natural Sciences of Philadelphia is labeled "Benicia." The remaining material is at the University of California, Berkeley and is labeled "8 M. N. of Yreka and Martinez." Anderson (1958, p. 156, pl. 29, fig. 1) chose a specimen from Thompson Creek, Yolo County (C.A.S. Loc. 31918) as the neotype. This designation must be considered invalid as the original material has not been lost even though not well preserved. In addition, Anderson's neotpye is not from any of the localities listed by Gabb.

Hypotype.—The figured specimen is number 28624 in the U.C.L.A. Invert. Paleo. Catalogue. Dimensions: height 52 mm.; height of spire 32 mm.; maximum width of body whorl 25 mm. Locality: U.C.L.A. 3474.

Remarks.—*Acteonina californica* Gabb is probably a *Trajanella* and is likely conspecific with our specimens (see pl. 101, fig. 30). Gabb's figure is an outline drawing that has a whorl profile that is more inflated than our specimen. The figure is labeled "natural size" and, therefore, represents a specimen considerably larger than the ones from the Bald Hills formation. The specimen figured by Stewart is but a longitudinal section through the shell. Stewart's figured specimen is about the same height as the specimen figured in this paper, but is wider and has a lower spire. Apparently all of Gabb's material was fragmentary and Stewart did not select a lectotype. He did, however, state that there is "considerable variation in the height of the spire of these specimens and they may include more than one species, . . . ". Although none of Gabb's material has been examined, a number of specimens of this genus collected by F. M. Anderson has been examined at the California Academy of Sciences. There is a great

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EXPLANATION OF PLATE 101

All figures natural size except as otherwise indicated.

FIGS. *1–4—Biplica* aff. *B. michaeli* Popenoe, *1,3*, two views of specimen 28651 U.C.L.A. Invert. Paleo. Cat. showing plication on columella and ornamentation and shape of shell; *2,4*, two views of specimen 28650 U.C.L.A. Invert. Paleo. Cat. showing excavated aperture and posterior plication, ×2.

5–8—Tornatellaea aff. *T. impressa* (Gabb). *5*, ornamentation of body whorl of specimen 28644 U.C.L.A. Invert. Paleo. Cat.; *6*, view illustrating spire of small specimen. U.C.L.A. Invert. Paleo. Cat. 28646; *7*, specimen 28645 U.C.L.A. Invert Paleo. Cat.; *8*, apertural view of specimen 28643 U.C.L.A. Invert. Paleo. Cat. showing columellar plication, ×2.

9–11—Ampullina stantoni n. sp. *9*, view illustrating shape of shell, ornamentation of body whorl of holotype U.C.L.A. Invert. Paleo. Cat. 28631; *10*, apertural view of specimen 28632 U.C.L.A. Invert. Paleo. Cat. showing umbilicus; *11*, view of specimen 28633 U.C.L.A. Invert. Paleo. Cat. showing shape of aperture, outer lip slightly damaged.

12,13—Ampullina mona n. sp. Two views of holotype; specimen 28634 U.C.L.A. Invert. Paleo. Cat.

14–17—Biplica isoplicata Popenoe. *14,15*, apertural views specimen 28647 U.C.L.A. Invert. Paleo. Cat. showing columellar plications; *16*, view showing spire and ornamentation of specimen 28649 Invert. Paleo. Cat.; *17*, view showing complete outer lip and ornamentation of specimen 28648 U.C.L.A. Invert. Paleo. Cat., ×2.

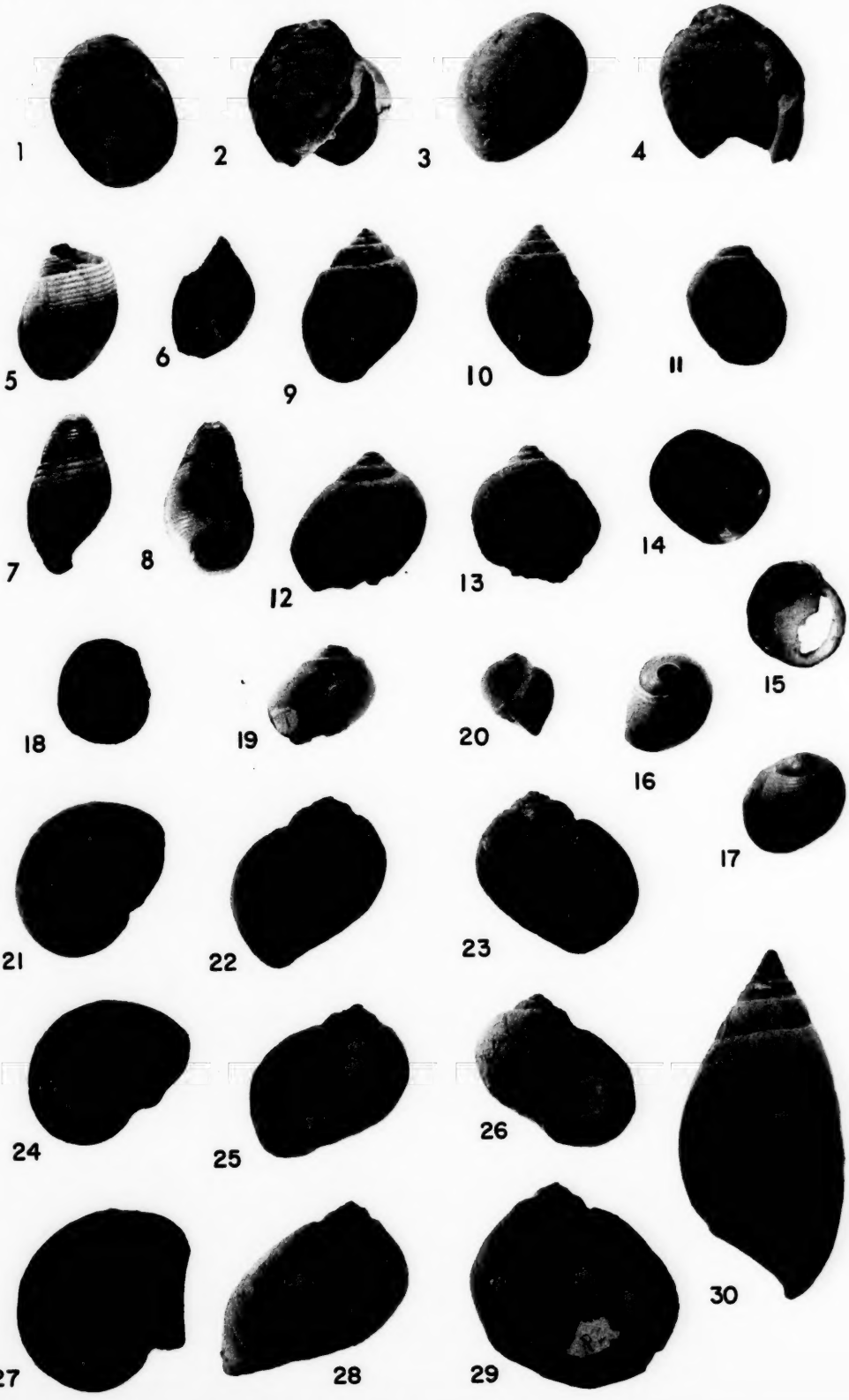
18–20—Gyrodes allisoni n. sp. *18,19* two views of holotype, 28629 U.C.L.A. Invert. Paleo. Cat., showing ornamentation and shape of shell; *20*, view of a small specimen, 28639 U.C.L.A. Invert. Paleo. Cat., showing the double angulation between the umbilicus and whorl flank.

21–23—Euspira popenoei n. sp. Three views of holotype, 28635 U.C.L.A. Invert. Paleo. Cat.

24–26—Euspira mariana n. sp. Three views of holotype, 28636 U.C.L.A. Invert. Paleo. Cat.

27–29—Gyrodes greeni n. sp. Three views of holotype, 28630 U.C.L.A. Invert. Paleo. Cat.

30—Trajanella californica (Gabb). Apertural view of specimen 28624 U.C.L.A. Invert. Paleo. Cat.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deal of variation in the inflation and spire height even in specimens from a single locality, but the growth line characteristics are the same in all specimens. Anderson (1958, p. 156) has recognized "*Acteonina*" *californica* Gabb from Thompson Creek, Yolo Co., and chose a specimen from this locality as the "neotype" of *A. californica* Gabb. Anderson (1958, p. 152–159) has also described seven new species: *A. ursula* and *A. ursulagorda* from the same locality on Bear Creek, on the east side of the Sacramento Valley; *A. bellavistana* from one mile North of Frazier Corners East of Redding; *A. berreyessaensis* from the same locality as *A. californica* above; *A. roguensis* from Phoenix, Oregon; *A. colusaensis* from the Peterson Ranch near Sites in Colusa County; *A. yrekensis* from Hagerdorn Ranch, Siskiyou County. It would probably be too much to expect that all these can be considered as one species as the lower occurrence is upper Albian for specimens from the Bald Hills formation, and probably Senonian (?) for *A. ursula* or *A. ursulagorda.* Yet examination of the collections fails to show any obvious reason for the separation of two or more species. The amount of variation between specimens from a single locality is as much as the variation among specimens of all localities.

Trajanella californica (Gabb) closely resembles the figure of *T. amphora* (d'Orbigny), the type of *Trajanella* (Cossmann, 1909, pl. 2, figs. 16–18), but is more inflated and has a lower spire. Some specimens of "*Acteonina*" *bellavistana* Anderson and "*A.*" *berreyessaensis* Anderson appear to be very similar to the genotype.

Large, accurately located stratigraphic collections will be necessary to obtain a more satisfactory solution to the taxonomic problem in this group. At present we do not feel that any of the described species can be used as an indication of stratigraphic position except in a broad sense.

Family APORRHAIDAE
Genus ARRHOGES Gabb, 1868
ARRHOGES CALIFORNICUS (Gabb)
Pl. 102, figs. 6,7

Aporrhais californica Gabb, 1864, p. 128, pl. 29, figs. 230 a,b.
Arrhoges californicus (Gabb), Stewart, 1926, p. 363, pl. 21, fig. 15.
Anchura (*Arrhoges*) *californica* (Gabb) Stewart, Anderson, 1958, p. 165.

Shell small, spire about ½ height of shell; number of whorls about 8; ornamentation consists of narrow longitudinal ribs shallowly concave toward the aperture and extending from just below the suture to the widest portion of the whorl, they number about 20 per whorl except on the body whorl where the number is reduced to 3 more pronounced ribs on the back of the whorl with the apertural side covered by

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EXPLANATION OF PLATE 102

FIGS. *1*—*Cantharus occidentalis* (Gabb) Apertural view of specimen 28637 U.C.L.A. Invert Paleo. Cat. ×1.

2—*Acteon sullivanae* n. sp. Apertural view of the holotype, 28642 U.C.L.A. Invert. Paleo. Cat. ×2.

3,4—*Cylichna andersoni* n. sp. *3*, view of specimen 28653 U.C.L.A. Invert. Paleo. Cat. showing the shape of the shell; *4*, apertural view of the holotype, 28652 U.C.L.A. Invert. Paleo. Cat. ×2.

5—*Clinura anassa* n. sp. Apertural view of the holotype, 28641 U.C.L.A. Invert. Paleo. Cat. ×1.

6,7—*Arrhoges californicus* (Gabb). *6*, apertural view of a small specimen, 28626 U.C.L.A. Invert. Paleo. Cat., showing spire and ornamentation of early whorls; *7*, adult specimen, 28625 U.C.L.A. Invert. Paleo. Cat., showing body whorl and partially preserved wing, ×2.

8,9—*Paleosephaea sacramentica* n. sp. *8*, oblique view of aperture of holotype, 28638 U.C.L.A. Invert. Paleo. Cat., showing the three columellar plications; *9*, view of specimen 28640 U.C.L.A. Invert. Paleo. Cat. showing ornamentation of shell. ×1.

10—*Mesopuzosia colusaense* (Anderson). Lateral view of specimen 28658 U.C.L.A. Invert. Paleo. Cat. Slightly less than natural size.

callus, shell surface covered by fine spiral lines with the two or three just below the suture much stronger than the others; on some specimens the longitudinal ribs are so reduced as to form a reticulate sculpture; growth lines are obscure on most of the shell, but the outer lip is ornamented only by growth lines; the first three whorls are unornamented; wing large, as wide as body whorl, with posterior rostrum nearly as high as spire; outer portion of wing thickened; anterior canal moderately long and rapidly tapering from body whorl; inner lip smooth with light callus.

Hypotypes.—The hypotypes, U.C.L.A. Invert. Paleo. Cat. nos. 28625 and 28626, were collected from locality 3465 on the North Fork of Cottonwood Creek. Dimensions of adult specimen: height 21 mm. (incomplete—lacks first whorl and top of anterior canal), height of spire 11 mm.; maximum thickness of last whorl (not including outer lip) 8 mm. (including outer lip) 16 mm.

Remarks.—The specimen figured by Stewart (1926, p. 363, pl. 21, fig. 15) is here designated as the lectotype of *Arrhoges californicus* (Gabb). The hypotypes have been compared with this specimen through the courtesy of H. Richards, of the Academy of Natural Sciences of Philadelphia who loaned us the type lot. The lectotype is "probably from the Siskiyou Mountains" (Stewart, 1926, p. 363). This species is very similar to specimens in the U.C.L.A. collection of *A. occidentalis* (Beck), the genotype, a Recent shell from the North Atlantic. This Cretaceous species is much smaller, has shorter longitudinal ribs, fewer spiral lirae, possesses two to three strong spiral ribs just below the suture, and has a slightly longer anterior canal.

Genus TESSAROLAX Gabb, 1864
TESSAROLAX TRINALIS n. sp.
Pl. 103, figs. 1,2,3

Shell small, moderately thick, spire about $\frac{1}{2}$ height of shell; body whorl biangulate with two rounded carina-like spiral ribs at the angulations and a third midway between; the upper rib is slightly stronger than the lower ribs and all may be slightly beaded; a single secondary rib may be developed between the posterior suture and the upper angulation; one or two secondaries may be developed below the lower angulation; the surface of young specimens is covered by fine lirae, in the adult the ornamentation is mostly covered with callus; number of whorls is greater than 5; suture linear, faint; aperture narrow above, widening below (anterior part unknown); in adult specimens the posterior digitation rises along the upper part of the shell obliquely and attached to the spire for about $\frac{2}{3}$ the length of spire and then is free of spire and directed away from aperture; anterior digitations not preserved; adult possesses tubercule-like knob $\frac{3}{4}$ of a turn back from the aperture, apparently a callus deposit.

Holotype.—The holotype, U.C.L.A. Invert. Paleo. Cat. no. 28627 was collected from locality 3763. Dimensions: height (incomplete) 19 mm., spire height 9 mm. (incomplete), greatest width (less apertural canals) 12 mm. Paratypr: U.C.L.A. Invert. Paleo. Cat. no. 28628.

Remarks.—This species differs from the genotype, *T. distorta* Gabb (1864, pl. 20, figs. 82,82a,b), in having three primary ribs on the body whorl and a much smaller tubercule-like process. *T. bicarinata* (Gabb) (Gabb, 1869, pl. 27, fig. 47; Stewart, 1926, pl. 23, fig. 6) is shorter, wider and has two heavy carinae with no intermediate rib.

The trivial name is from Latin, three.

Genus GYRODES Conrad, 1860
GYRODES ALLISONI n. sp.
Pl. 101, figs. 18,19,20

Shell thin, small to medium size; spire about $\frac{1}{5}$ the height of the shell; number of whorls about 4; subangular shoulder and wide posterior tabulation; tabulation flat to very shallowly grooved; ornamentation of spiral lines, very fine on most of the whorl, and strongly developed on the posterior tabulation; growth lines fine but distinct; sharp double angulation at the edge of the umbilicus, band between angulations flat to depressed and nearly as wide at the umbilical opening; suture impressed; aperture elongate oval.

Holotype.—The holotype and paratype, U.C.L.A. Invert. Paleo. Cat. nos. 28629 and 28639, respectively, were collected at locality 3464 near the Gas Point road. Dimensions of the holotype: height 13 mm., height

of spire 2½ mm.; maximum width of last whorl 12 mm.

Remarks.—This species most nearly resembles "*Gyrodes*" *siskiyouensis* Anderson (1958, p. 150, pl. 21, figs. 6,7) in ornamentation, but has a more prominent shoulder, and a flattened or slightly concave flank below the shoulder. The umbilical characteristics of *G. siskiyouensis* are not known. This species differs from other California forms in the ornamentation of the tabulation.

This species is named for Edwin Allison, Department of Paleontology at the University of California, Berkeley.

GYRODES GREENI n. sp.
Pl. 101, figs. 27,28,29

Shell medium to large, heavy; spire about ⅙ the height of the shell; number of whorls 4–5; angular shoulder with narrow tabulation; suture impressed; ornamented only by growth lines; very sharp single angulation along the umbilical edge; umbilicus wide, open; aperture broadly comma-shaped.

Holotype.—The holotype, U.C.L.A. Invert. Paleo. Cat. no. 28630 was collected from locality 3465 near the North Fork of Cottonwood Creek. Dimensions; height, 30 mm.; height of spire 5 mm.; maximum width of last whorl 31 mm.

Remarks:—*Gyrodes greeni* resembles *Gyrodes expansa* (Gabb) (Stewart, 1926, pl. 22, figs. 1,1a), but the latter species has a much wider tabulation, a broader spire and a rounded angulation at the umbilical edge. Small specimens of *G. greeni* n. sp. resemble topotypes of *G. canadensis* Whiteaves (1879, pl. 16, figs. 2,2a), but lack the sub-shoulder constriction, the groove in the tabulation, and the double angulation of the umbilical edge that are present on the latter species.

The species is named for A. L. Green, Ono, California.

Genus AMPULLINA Bowdich, 1822
AMPULLINA STANTONI n. sp.
Pl. 101, figs. 9,10,11

Shell thick, medium-sized; spire about ⅜ height of the shell; ornamentation is of prominent growth lines on last whorl, occasional specimens with very faint spiral striation; number of whorls about 5; whorl profile gently rounded with a tendency for the last volution to be slightly flattened on the posterior half of the whorl; aperture similar to the genotype but more elongate and columellar wall more curved; umbilicus elongate, narrow, eye-shaped slit; moderate callus on the inner lip.

Holotype.—The holotype and paratypes, U.C.L.A. Invert. Paleo. Cat. nos. 28631, 28632, 28633, respectively, were collected at U.C.L.A. locality 3763. Dimensions of holotype: height of shell 24 mm.; width of body whorl 17 mm.; height of spire 9 mm.

Remarks.—*A. stantoni* n. sp. resembles *Lunatia avellana* Gabb (1864, pl. 19, fig. 60) but does not resemble the plate of Stewart's lectotype of *Ampullina avellana* (Gabb) (1926, pl. 21, fig. 9). Gabb's figure shows the slight bending of the inner lip which is characteristic of *A. stantoni* n. sp. and Stewart's does not. Stewart's lectotype appears to be more globose. The umbilicus of *A. stantoni*, while small, is not as Gabb states for *A. avellana*, "barely visible."

A. stantoni n. sp. was found abundantly at localities 3473 and 3765 in the Bald Hills formation and also with the *Brewericeras hulenense* fauna near Clear Creek near the site of the old mining camp of Horsetown.

The species is named for T. W. Stanton, pioneer worker in California Mesozoic paleontology.

AMPULLINA MONA n. sp.
Pl. 101, figs. 12,13

Shell globose, thick, medium-sized; spire ⅜ height of shell; faint spiral lines at shoulder, rest of shell smooth except for growth lines; number of whorls 4; suture impressed; aperture comma-shaped, widest just above the base (anterior end missing); umbilicus a short narrow depressed area; moderate callus on the inner lip.

Holotype.—The holotype and only specimen, U.C.L.A. Invert. Paleo. Cat. no. 28634 was collected from locality 3778 on Huling Creek about 5 feet above the conglomerate at the base of the Bald Hills formation. Dimensions: height (incomplete) 21 mm.; greatest diameter of body whorl 20 mm.; height of spire (incomplete) 6 mm.

Remarks.—This species is not as tall as *A. stantoni*, is more inflated and has a lower spire. The umbilicus is not open as it is in *A. stantoni* and the callus on the inner lip is

much heavier. *A. avellana* (Gabb) has a smaller, thinner shell with a higher spire and a lighter callus than *A. mona* n. sp.

This species is named for Mrs. Ramona Rodda.

Genus EUSPIRA Agassiz, 1839
EUSPIRA POPENOEI n. sp.
Pl. 101, figs. 21,22,23

Shell moderately thick, medium-sized; spire about $\frac{1}{4}$ the height of the shell; smooth except for growth lines and very fine spiral striae that are most often preserved on the younger whorls; number of whorls about 5; body whorl slightly flattened above the middle; junction between umbilical wall and whorl flank angulate; suture impressed; aperture nearly semicircular with very slight notch or gutter at the posterior suture; umbilicus moderate size; callus restricted to inner lip.

Holotype.—The holotype, U.C.L.A. Invert. Paleo. Cat. no. 28635, was collected at locality 3464 near the Gas Point road. Dimensions: height 26 mm.; spire height 6 mm.; greatest width 24 mm.

Remarks.—Euspira popenoei n. sp. differs from *Euspira marianus* n. sp. in having a smaller umbilicus, an angulation between the umbilical wall and the flank, and an impressed suture. *Euspira popenoei* n. sp. differs from the lectotype of *Polinices shumardianus* (Gabb) Stewart (1926, pl. 21, fig. 11) in lacking the partially closed umbilicus, in being taller, in having a more elongate aperture and in having an angulation at the umbilical edge.

This species is named for W. P. Popenoe of the University of California, Los Angeles.

EUSPIRA MARIANUS n. sp.
Pl. 101, figs. 24,25,26

Shell moderately thick, medium-sized; spire about $\frac{1}{3}$ height of the shell, number of whorls about five; body whorl flattened above the middle; faint shoulder and tabulation near the posterior suture; shell smooth except for growth lines and fine spiral striae faintly developed on the shoulder; suture impressed; aperture nearly semicircular; umbilicus large, open; narrow flattened area between true umbilical depression and flank, somewhat like the double angulation of *Gyrodes allisoni* n. sp., but set off from flank and umbilicus by abrupt change in the curvature of the shell rather than by distinct angulations; callus restricted to inner lip.

Holotype.—The holotype, U.C.L.A. Invert. Paleo. Cat. no. 28636, was collected at locality 3465 near the North Fork of Cottonwood Creek. Dimensions: height 25 mm.; spire height 5 mm.; greatest width 25 mm.

Remarks.—Differs from *E. popenoei* in having faint tabulation and shoulder near the posterior suture and a larger umbilicus and in lacking an angulate umbilical edge. Differs from *Polinices shumardianus* (Gabb) in having an open umbilicus.

It is very difficult to give generic assignments to *E. popenoei* and *E. marianus*. The type specimens are so close that one would certainly not separate them generically, yet each resembles a different genus. *E. popenoei* most resembles the type of *Euspira*, *Euspira labellata* (Lamarck), in general shape, but has a more impressed suture, a more retracted growth line, a more open umbilicus (slightly), bounded by an angulation, and the callus does not extend across and above the umbilicus as in *Euspira*. *E. marianus* resembles the type of *Gyrodes* (*Sigaretopsis*), *G.* (*S.*) *infundibulum* (Watelet), but has a more channeled suture, the growth lines are not inclined forward so strongly, possesses definite, but weak, double angulation at the edge of the umbilicus (somewhat like *Gyrodes* s.s.), and the callus does not extend across above the umbilicus. *E. marianus* very closely resembles specimens in the U.C.L.A. collection from the Gault of Folkestone, England labeled, *Gyrodes genti* (Sowerby), but these specimens have a more impressed suture and a wider, but less angulate umbilicus. *E. marianus* would seem to be closely allied to *Gyrodes* while one would hesitate to put *E. popenoei* in *Gyrodes*. Assignment to *Euspira* is questionable.

Gyrodes pluvianus Stephenson (1952, p. 152, pl. 36, p. 20–23) is similar to this species, but appears to have a larger umbilicus with a more pronounced angulation, and a lower spire.

The species is named for Andrew Marianos, micro-paleontologist for the Humble Oil and Refining Company, Chico, California.

Family BUCCINIDAE
Genus CANTHARUS Roding, 1798
CANTHARUS OCCIDENTALIS (Gabb)
Pl. 102, fig. 1

Fusus occidentalis Gabb, 1869, p. 146, 215, pl. 26, fig. 23.
Pseudoperissolax (?) *occidentalis* (Gabb), Stewart, 1926, p. 430, pl. 21, fig. 1.

One incomplete but well preserved specimen from the Bald Hills formation has been compared to the holotype (Stewart, 1926, pl. 21, fig. 8) and is believed to be conspecific. However, our specimen has a single strong varix along the outer margin of the aperture and another weakly formed about ⅔ of a revolution behind. The possession of a varix is probably a variable feature as neither Stewart's nor Gabb's figures show varices, nor does either author mention them, and they are not present on other specimens in our collections referred to this species.

Holotype.—The type specimen is reported to come from Martinez, but this has not been confirmed.

Figured specimen.—The figured specimen, U.C.L.A. Invert. Paleo. Cat. no. 28637 was collected from locality 3465 near the North Fork of Cottonwood Creek. The species also occurs at U.C.L.A. locality 3816 above the Bald Hills formation. Dimensions: height 18.5 mm.; height of spire (incomplete) 8.5 mm.; maximum width of last whorl 13 mm.

Family VOLUTIDAE
Genus PALEOPSEPHAEA Wade, 1926
PALEOPSEPHAEA SACRAMENTICA n. sp.
Pl. 102, figs. 8,9

Shell medium sized, heavy, fusiform; spire height about ½ height of shell; number of whorls about 5; axial ornamentation of elongate ribs extending from suture to suture except on body whorl where ribs die out on the anterior slope, 12 ribs on last whorl, 11 on penultimate whorl, concave aperturally; spiral sculpture of fine spiral lines most prominent on posterior slope; faint growth lines parallel the axial ribs; aperture elongate, narrowly rounded posteriorly; outer lip simple, broadly convex; inner lip concave posteriorly, broadly convex anteriorly, with a thin callus; columella bears three oblique folds; the anterior fold is slightly stronger and the posterior slightly weaker than the median fold.

Holotype.—The holotype, U.C.L.A. Invert. Paleo. Cat. no. 28638, was collected at locality 3474 on Coyote Creek. Dimensions: height of the whorl (incomplete) 35 mm.; height of spire (incomplete) 18 mm.; maximum width of last whorl 14 mm. Fig. 9 is a larger specimen collected above the Bald Hills formation at locality 3817, and is the paratype, U.C.L.A. Invert. Paleo. Cat. no. 28640.

Remarks.—This is the first record of this genus in the California Cretaceous. The specimens agree with the description and figures of the genotype, *P. mutabilis* Wade (Wade, 1926, p. 123, pl. 40, figs. 4,5,8). *P. sacramentica* n. sp. is slenderer and has smaller and more abundant axial ribs than the genotype, and the anterior columellar fold is not as strong. *P. sacramentica* n. sp. differs from *P. decorosa* Stephenson and *P. patens* Stephenson (1952, pl. 41, figs. 23–26) from the Woodbine formation of Texas in being a smaller shell and having the anterior columellar fold the largest of the three.

The species derives its name from its occurrence in the Sacramento Valley.

Family TURRIDAE
Genus CLINURA Bellardi, 1875
CLINURA ANASSA n. sp.
Pl. 102, fig. 5

Shell medium-sized, moderately thick, fusiform; spire elevated and acute, about ½ the height of the shell; number of whorls (incomplete) almost 5; suture impressed; axial sculpture of 10–12 strong nodes per whorl on the angulation; irregular, narrow axial ribs extend below the angulation and form beads where they cross the primary spiral ribs; spiral ornamentation of 3 evenly spaced coarsely beaded, primary spiral ribs in the upper half of the lower flank below the angulation; surface covered by spiral lirae; growth lines prominent and reflect broad shallow notch on the upper flank of the whorl above the angulation; columella smooth, twisted, with light callus on inner lip; anterior incomplete on all specimens.

Holotype.—The holotype, U.C.L.A. Invert. Paleo. Cat. no. 28641, was collected at locality 3476 on Coyote Creek. Dimensions: height (incomplete) 23.5 mm.; height

of spire (incomplete) 11.5 mm.; maximum width of last whorl 12 mm.

Remarks.—This species is similar to *Clinura io* (Gabb) (Gabb, 1864, pl. 28, fig. 214) from the Eocene (Tejon) of California, but differs in the following ways: *Clinura anassa* n. sp. is slightly taller and slimmer, has more abundant and slightly more subdued nodes on the angulation, fewer primary spiral ribs on the lower flank (3–4 as compared to 10–12 for *C. io*), a convex whorl profile on the upper half of the lower whorl, and no sutural collar.

This is apparently the oldest record of the family Turridae as defined by Wenz (1943, p. 1380). Previously described species of *Clinura* are Eocene or younger.

The trivial name is from Greek, queen.

Family ACTEONIDAE
Genus ACTEON Monfort, 1810
ACTEON SULLIVANAE n. sp.
Pl. 102, fig. 2

Shell, small, high spired; spire about ½ height of shell; number of whorls about 6; suture impressed; ornamentation consists of spiral grooves which are strongest near the anterior and become weaker posteriorly except for three just below the suture; surface covered by fine lines of growth; aperture elongate, narrowest posteriorly; inner lip with a light callus; columella with a single small fold situated at the juncture of the columellar and parietal lips.

Holotype.—The holotype and only specimen, U.C.L.A. Invert. Paleo. Cat. no. 28642, was collected at locality 3768 east of the old Gas Point Road. Dimensions: height 8.5 mm.; height of spire 4.2 mm.; maximum width of last whorl 3.7 mm.

Remarks.—*Acteon sullivanae* n. sp. is similar to *A. politus* (Gabb), but differs from the lectotype (Stewart, 1926, p. 341, pl. 24, fig. 18) of the latter in being narrower and in having a higher spire and more numerous spiral ribs with a wide smooth band on the posterior ⅓ of the whorl.

The species is named for Mrs. Catherine Sullivan on whose ranch it was found.

Genus TORNATELLAEA Conrad, 1860
TORNATELLAEA sp. aff. T. IMPRESSA (Gabb)
Pl. 101, figs. 5,6,7,8

Acteon impressus Gabb, 1864, p. 142, pl. 21, fig 106.

Specimens very close to *T. impressa* Gabb have been found at several localities in the Bald Hills formation. These agree well with Stewart's figured specimens (1926, pl. 24, figs. 7,8) in size and shape, but have smaller more abundant spiral ribs, and the ornamentation is not subdued or absent on the upper third of the whorl. This species occurs throughout the Bald Hills formation and in the formation immediately above as well.

The figured specimens are, U.C.L.A. Invert. Paleo. Cat. nos. 28643, 28644, 28645, 28646 and were collected at U.C.L.A. locality 3476.

Genus BIPLICA Popenoe, 1957
BIPLICA ISOPLICATA Popenoe
Pl. 101, figs. 14,15,16,17

Biplica isoplicata Popenoe, 1957, p. 434–435, pl. 50, figs. 12–17.

Specimens from eleven localities in the Bald Hills formation have been assigned to this recently described species (Popenoe, 1957, p. 434–35, pl. 50, figs. 12–17). Stratigraphically these specimens occur between the listed occurrences of *Biplica michaeli*, a lower Albian species, and *B. isoplicata*, a Turonian form. Some of the specimens from locality 3476 are notably larger than any specimen of *B. isoplicata* previously reported but are otherwise similar. The species is abundant throughout the Bald Hills formation.

Types.—The holotype, U.C.L.A. Invert. Paleo. Cat. no. 27742, was collected at U.C.L.A. locality 3287. The hypotypes, U.C.L.A. Invert. Paleo. Cat. nos. 28647, 28648, 28649, are from U.C.L.A. locality 3476.

BIPLICA aff. B. MICHAELI Popenoe
Pl. 101, figs. 1,2,3,4

Biplica michaeli Popenoe, 1957, p. 433–434, pl. 50, figs. 9–11.

Specimens of the genus *Biplica* from locality 3763 in the Bald Hills formation are considered to have affinities for *B. michaeli* Popenoe. Small specimens at this locality (altitude 4.0–5.4 mm.) agree with this species in essential details except that they have a slightly lower spire. At the same locality large specimens (altitude 7.5–11.0 mm.) have proportions similar to *B. michaeli*, but are much larger. In fact, these specimens are larger than any representa-

tives of *Biplica* known below the uppermost Santonian (?) or lowermost Campanian (?) (Popenoe, 1957, fig. 1). These large specimens lack the third tooth-like projection on the posterior end of the inner lip of *B. michaeli*. This feature, however, is not considered as diagnostic as shape and spire height (Popenoe, oral communication, 1958). The third tooth-like projection is known only from the holotype of *B. michaeli*. It is to be expected that the limits of variation of *B. michaeli* may be greatly extended as its hypodigm consists of only four specimens.

The difference in stratigraphic position and size of *B. michaeli* and *B.* aff. *michaeli* is such that it seems best to reserve judgment on the specific identification of these specimens until the variability of *B. michaeli* is better known.

Figured specimens.—U.C.L.A. Invert. Paleo. Cat. nos. 28650 and 28651.

Family SCAPHANDRIDAE
Genus CYLICHNA Loven, 1846
CYLICHNA ANDERSONI n. sp.
Pl. 102, figs. 3,4

Shell very small, elongate, cylindrical; spiral sunken in pit in top of shell; number of whorls about 3; apex truncated and very flat; spire pit about $\frac{1}{2}$ diameter of the truncated apex; ornamentation of fine spiral lines widely spaced and prominent on the anterior half of the whorl with a few closely spaced spiral lines immediately above and below the posterior angulation; very fine spirals occasionally present on the rest of the whorl; fine growth lines. Small crenulation immediately below the posterior angulation; aperture narrow linear, outer lip vertical, inner lip appears to be without callus; basal portion of aperture evenly rounded, projects slightly below base of columella.

Types.—The holotype and paratype, U.C.L.A. Invert. Paleo. Cat. nos. 28652 and 28653, respectively, were collected at locality number 3476 on Coyote Creek. Dimensions of the holotype: height $3\frac{1}{2}$ mm., maximum width 2 mm.

Remarks.—No species close to this has been previously described from the California Cretaceous. Stewart's choice of a lectotype from Martinez for *Cylichna costata* Gabb places that species in *Scaphander*. Gabb mentions other Cretaceous localities under *C. costata*, but the specimens have not been found (Stewart, 1926, p. 440).

The species is named for F. M. Anderson, former curator of the California Academy of Sciences.

Class CEPHALOPODA
Order AMMONOIDEA Zittel, 1884
Family TURRILITIDAE Meek, 1876
Genus PSEUDHELICOCERAS Spath, 1921
PSEUDHELICOCERAS PETERSONI (Anderson)
Pl. 107, figs. 1,2,3

Turrilites petersoni Anderson, 1958, p. 193, pl. 12, fig. 6, pl. 75, fig. 4.
Pseudohelicoceras petersoni (Anderson), Matsumoto, 1958, p. 651.

Coiling dextral, loose, successive whorls not in contact; ornamentation of light ribs and tubercles; ribs rursiradiate, inflected slightly posteriorly on the posterior side of the whorl, interrupted on the flanks in part by four spiral rows of tubercles; tubercles broad, low blister-like, arranged in four spiral rows and placed en echelon one above the other on the flanks and anterior part of the shell so that they parallel the ribs; two or three ribs are interrupted by each tubercle and two or three ribs pass across the flank uninterrupted between the tubercles; suture complex, L narrow, deep, bifid, undercutting the first lateral saddle and E, E about $\frac{2}{3}$ as deeply incised as L (Pl. 107, fig. 3).

Hypotype.—The hypotype is specimen number 28722 U.C.L.A. Invert. Paleo. Cat. It was collected at U.C.L.A. locality 3775 in the lowest conglomerate unit of the Bald Hills formation on the North Fork of Cottonwood Creek. The specimen was in a limy sandstone clast in the conglomerate.

Remarks.—The suture differs markedly from that of the genotype, *P. robertianum* (d'Orbigny), as figured by d'Orbigny (1842, pl. 142) in that L is much larger than and undercuts E. The reverse is true in the genotype.

Range.—The true stratigraphic occurrence of the species is probably not later than upper Albian, the highest known occurrence of the genus.

PSEUDHELICOCERAS sp.

A single specimen of *Pseudhelicoceras* was found at U.C.L.A. locality 3778 about 5 feet stratigraphically above the lowest conglomerate of the Bald Hills formation exposed on

Huling Creek. The specimen is sinistrally coiled and half again as large as the specimen described under *Pseudhelicoceras petersoni* (Anderson) and probably represents a different species. It is noted here because it is the only specimen found above the lowest conglomerate unit of the Bald Hills formation that is the member of a taxonomic group restricted to the Albian. It is, therefore, on the evidence of this single specimen that we date the lowermost unit of the Bald Hills formation on the North Fork of Cottonwood Creek and Huling Creek as uppermost Albian.

The specimen was found in nodular limestone in mudstone matrix. It is number 28723 U.C.L.A. Invert. Paleo. Cat.

Genus MARIELLA Nowak, 1916

MARIELLA (MARIELLA) FRICKI n. sp.

Pl. 103, fig. 7

Turrilites bergeri Brongniart, Anderson, 1958, p. 193, pl. 11, fig. 2.

Apical angle 34°; the whorl is ribbed from unbilical edge to the upper whorl suture; ribs are less well defined on the posterior quarter of the whorl; each rib has four prominences with the lower three approximately equal in size and somewhat smaller than the upper; the upper prominence is bullate, the middle two are more tuberculate than bullate, while the lower tends to be slightly bullate; the upper three rib prominences are equidistant whereas the lower is slightly more closely spaced; in the younger states of growth the prominences are sharper and more spiny; cross-section of the whorl is egg-shaped.

Holotype.—The holotype, specimen number 28654 U.C.L.A. Invert. Paleo. Cat., was collected at locality 3467 from the lowest conglomerate bed of the Bald Hills formation exposed on the North Fork of Cottonwood Creek. The specimen was enclosed in nodular limestone, probably a clast in the conglomerate. Dimensions: height (incomplete) 45 mm., maximum width 33 mm., height of whorl 20 mm., width 16 mm., apical angle 34°.

Remarks.—This is the first species of the genus described from California. It differs from the genotype *M. bergeri* Brongniart, in having a much larger apical angle.

M. (M.) fricki resembles *Turrilites bergeri* Brongniart (Sharpe, 1856, pl. 26, fig. 10) (=*Paraturrilites lewesiensis* Spath, Wright and Wright, 1951, p. 40), but in Sharpe's figure the posterior portion of the whorl appears to be smooth, unlike *M. (M.) fricki* which possesses posterior ribs.

The specimen figured by Anderson (1958, pl. 11, fig. 2) is crushed but apparently represents the same species although found somewhat higher in the section.

The species is named for Master John Frick of Chico, California, who found the holotype while in the company of the writers.

EXPLANATION OF PLATE 103

FIGS. *1–3*—*Tessarolax trinalis* n. sp. *1*, holotype, 28627 U.C.L.A. Invert. Paleo. Cat., showing the character of posterior canal; *2,3*, two views of a smaller specimen, 28628 U.C.L.A. Invert. Paleo. Cat., showing the ornamentation of the spire, ×2.

4,5—*Solariella stewarti* n. sp. *4*, apertural view of the holotype, 28622 U.C.L.A. Invert. Paleo. Cat; *5*, oblique view of the spire of specimen 28623 U.C.L.A. Invert. Paleo. Cat. showing the ornamentation of the shoulder, ×2.

6—*Turrilites dilleri* n. sp. Holotype, 28655 U.C.L.A. Invert. Paleo. Cat., ×1.

7—*Mariella fricki* n. sp. Holotype, 28654 U.C.L.A. Invert. Paleo. Cat., ×1.

8—*Mortoniceras gainesana* (Anderson). Lateral view of specimen 28674 U.C.L.A. Invert. Paleo. Cat., approximately ⅓ natural size.

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Genus TURRILITES Lamarck, 1801
TURRILITES (TURRILITES) DILLERI n. sp.
Pl. 103, fig. 6

Apical angle about 21°; the whorl is ornamented by three rows of bullate or tuberculate prominences which are connected by faintly developed transverse ribs that extend from slightly below the lower row of prominences to the upper whorl suture; the lower prominence is elongate slightly in a direction about 60° from the direction of the axis of coiling; the middle prominence is more or less equidimensional; the upper prominence is elongate in a direction at a slight angle to the axis of coiling; maximum length of shell probably exceeded 3 inches.

Holotype.—The holotype, specimen number 28655 in the U.C.L.A. Invert. Paleo. Cat., consists of two complete whorls of a completely septate shell with a maximum diameter of 18 mm. The holotype and three other specimens were collected from U.C.L.A. locality 3464. All four have virtually the same characteristics of ornamentation even though each specimen represents a different growth stage.

Remarks.—*Turrilites* (*Turrilites*) *dilleri* n. sp. differs from *T. oregonensis* Gabb (1864, pl. 28, fig. 201) in having only 3 rows of prominences rather than 4. "*Turrilites*" *Carlottensis* Whiteaves (1900, pl. 34) probably belongs to *Emperoceras* or some closely related genus. *T. dilleri* n. sp. differs from the genotype, *T. costatus* Lamarck, in the proportions of the bullae and a much less prominent spiral trough separating the posterior bulla from the anterior ones.

T. (*T.*) *dilleri* closely resembles two of Sharpe's figures of *Turrilites, T. costatus* Lamarck (Sharpe, 1856, pl. 27, fig. 1), and *T. wiestii* Sharpe (pl. 27, fig. 8). Both of these specimens have been referred to *T. acutus* Passy by Wright and Wright (1951, p. 40). *T. dilleri* appears to be more loosely coiled than these specimens. In Sharpe's figures the lower bulla is not visible when the succeeding coil is present, but it is visible on *T. dilleri.*

The species is named for J. S. Diller pioneer worker in northern California geology.

Family DESMOCERATIDAE Zittel, 1895
Genus PUZOSIA Bayle, 1878
PUZOSIA PUMA n. sp.
Pl. 104, figs. 5,6

Shell compressed with a high, flat-sided whorl cross section; umbilicus wide and shallow in comparison to most members of the genus (25 mm. at a diameter of 73 mm.); umbilical edge sharply rounded; umbilical wall low, steep, abutting previous whorl at umbilical seam; ornamentation consists of sigmoidal constrictions and ribs; the constrictions number about 5 per whorl, are deep and prominent from umbilical seam to umbilical seam, cross the venter with a pointed anterior inflection, show on the external shell as shallow groves preceded by a low labial ridge; constrictions are inflected forward at a greater angle than the intervening ribs, and, therefore, intersect several of the anteriormost ribs of each intra-constriction space; between each constriction are about 13 subdued sigmoidal ribs that arise near the lower quarter of the flank and cross the venter without interruption. The suture line is not exposed on the inner half

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EXPLANATION OF PLATE 104

All figures ×1

FIGS. *1–3*—*Eogunnarites matsumotoi* n. sp. *1*, cross-section view of holotype, 28664 U.C.L.A. Invert. Paleo. Cat.; *2*, lateral view of holotype; *3*, fragment of body whorl of the holotype.

4—*Beudanticeras haydeni* (Gabb). View of specimen 28660 U.C.L.A. Invert. Paleo. Cat. showing first lateral lobe of suture.

5,6—*Puzosia puma* n. sp. Ventral and lateral views of the holotype, 28656 U.C.L.A. Invert. Paleo. Cat.

of the flank, but the first lateral lobe is trifid, complexly frilled, and about twice as deep as the external lobe and very similar to the corresponding elements in the genotype as figured by Wright (1957, p. L364, fig. 476–5c). The maximum size was probably over 8 inches in diameter as the holotype measures more than 6 inches in diameter (reconstructed) and is septate throughout.

Holotype.—The holotype is specimen number 28656 U.C.L.A. Invert. Paleo. Cat. It was collected at locality 3477 on Coyote Creek. Dimensions: height of whorl 27 mm., width of whorl 16 mm. (approximate), width of umbilicus 25 mm. All measurements at 73 mm. diameter.

Remarks.—*P. puma* n. sp. can be differentiated from other puzosids described from California by its high flat-sided whorl, wide shallow umbilicus and low, acutely rounded umbilical wall.

In addition to the locality of the holotype, the species has been found in the mudstones overlying the Bald Hills formation in the North Fork of Cottonwood Creek area.

The trivial name is a synthetic word.

PUZOSIA SULLIVANAE n. sp.
Pl. 105, figs. 4,5

Shell medium size with an ovate almost equant adult whorl section; umbilicus a little less than one third diameter of shell; umbilical edge rounded; umbilical wall steep, convex, turned under at the umbilical seam; ornamentation consists of sigmoidal constrictions and ribs; constrictions 5 per whorl, moderately deep grooves on the internal mold, cross the venter with a slight anterior inflection, reflected on the external shell; ribs between each constriction variable in number (19–27), very low and indistinct on the periphery and absent on the inner half of the flank to about 50 mm. diameter; ribs on the early part of the body whorl reach the umbilical edge, may bifurcate on the shoulder or arise by intercalation on the shoulder; suture puzosid, complexly frilled.

Holotype.—The holotype, specimen number 28657 U.C.L.A. Invert. Paleo. Cat., was collected at U.C.L.A. locality 3764 by W. P. Popenoe. It is the only known specimen. Dimensions: at 77 mm. diameter, height of whorl 32 mm., width of whorl 30 mm., umbilicus diameter 23 mm.

Remarks.—*Puzosia sullivanae* n. sp. resembles *P. dilleri* (Anderson) (Anderson, 1938, pl. 42, fig. 1, not pl. 42, figs. 2,3) more closely than any of the other California species but has a much smaller umbilicus than the latter.

The species is named for Mrs. Catherine Sullivan near whose ranch the holotype was found.

Genus MESOPUZOSIA Matsumoto, 1954
MESOPUZOSIA COLUSAENSE (Anderson)
Pl. 102, fig. 10

Desmoceras colusaense Anderson, 1902, p. 96,97. pl. v, figs. 128,129, pl. x, fig. 200.
Puzosia (Parapuzosia) colusaense (Anderson), Anderson, 1958, p. 236, pl. 10, fig. 1.
Pachydesmoceras colusaense (Anderson), Matsumoto, 1958, p. 652.

Shell large with ovate whorl section; umbilicus a little less than $\frac{1}{3}$ diameter of the shell; umbilical edge smooth, rounded; umbilical wall steep, rounded (convex), turned under at the umbilical seam; ornamentation of sigmoidal constrictions and ribs; the constrictions number 6 or 7 on specimens about 150 mm. in diameter, more constrictions per whorl (about 10) are apparently present on the younger shell judging from a partially preserved specimen of about 50 mm. diameter; Anderson (1902, p. 97) reported 10–11 constrictions on the young whorls of his specimen; number of ribs between each constriction varies greatly with growth, on specimens of about 150 mm. diameter, 17–19 ribs are on the periphery, 10–13 on the flanks; ribs reach almost to the umbilical edge; suture puzosid, Anderson's figure (1902, pl. 10, fig. 200) is good for the external lobe, 1L and the outer part of the suspensive lobe.

Holotype.—The holotype is type specimen number 4283 in the collections of the California Academy of Sciences in San Francisco. It was found on the Petersen Ranch 4 miles north of Sites, Colusa County, California.

Remarks.—If the position of the ribs on the flank and the flatness of the flank be treated as definitive characters, this species cannot be placed in the genus *Puzosia*. It does not have the features of ornamentation cited by Wright (1957, p. L365) for *Pachy-*

desmoceras. It seems to resemble *Mesopuzosia* in most of its features but the ribs do not reach the umbilical edge. If the species is assigned to *Mesopuzosia*, it extends the range of that genus down to the uppermost Albian from Turonian. It may be that this species is transitional between *Puzosia* and *Mesopuzosia*. In any case, the generic assignment is based on morphologic similarity and *Mesopuzosia* seems to be morphologically the most similar group.

Range.—This species has a restricted stratigraphic position and is probably uppermost Albian in age. It is found with *Pseudhelicoceras*, *Desmoceras* (*Pseudouhligella*), *Mortoniceras*, *Mariella*, *Eogunnarites*, and *Anisoceras* in clasts in the lowest conglomerate of the Bald Hills formation on the North Fork of Cottonwood Creek. It also occurs free in the matrix of this unit. It occurs in limestone nodules on the same horizon as *Pseudhelicoceras* cf. *P. petersoni* (Anderson) in the mudstone unit immediately above the conglomerate. *Desmoceras* (*Pseudouhligella*) and *Zelandites* occur both stratigraphically above and below the known occurrences of this species.

M. colusaense (Anderson) is recorded from the Peterson Ranch near Sites, Colusa County and from Dry Creek in Tehama County, as well as the North Fork of Cottonwood Creek localities listed in this paper.

Genus BEUDANTICERAS Hitzel, 1905
BEUDANTICERAS HAYDENI (Gabb)
Pl. 104, fig. 4, Pl. 105, figs. 1,2.

Ammonites haydeni Gabb, vol. I, 1864, p. 62, pl. 10, figs. 8,8a.

Desmoceras (*Puzosia*) *Haydeni* (Gabb), Whiteaves, 1900, vol. 1, pt. 4, p. 285; ? Anderson, 1902, p. 41; Hanna and Hertlein, 1943, fig. 61–8.

Beudanticeras haydeni (Gabb), Anderson, 1938, p. 190 in part, not pl. 48, figs. 2,3; Murphy, 1956, p. 2119, fig. 6; Anderson, 1958, p. 212, pl. 8, fig. 1,1a.

The holotype, no. 14973 in the Museum of Paleontology, University of California, Berkeley, was found on the North Fork of Cottonwood Creek, Shasta County, California. F. M. Anderson has notes with this specimen stating that it is not the type, but it agrees in detail with Gabb's figures and is regarded as the holotype in this paper. Anderson's figured specimens (1938, pl. 48, figs. 2,3) are small specimens of *Brewericeras hulenense* (Anderson).

Beudanticeras haydeni (Gabb) has a compressed shell, narrowly rounded venter and a flank that is broad in relation to the small umbilicus. The ornamentation consits of falciform growth lines and periodic, low, crescent-shaped ridges on the peripheral half of the flank. The suture line (pl. 4, fig. 4) is virtually identical with that figured in Spath (1923, text fig. 12c) for *Beudanticeras beudanti*. The umbilical wall and flank meet at right angles to one another at the sharply angular umbilical edge. Specimens up to eight inches in diameter are in our collection, but the average specimen is about four inches in diameter.

Hypotypes.—Specimen 28659 U.C.L.A. Invertebrate Paleo. Cat. was collected from the lowest conglomerate of the Bald Hills formation on the North Fork of Cottonwood Creek, U.C.L.A. locality 3467. Specimen 28660 U.C.L.A. Invert. Paleo. Cat. was collected in the *Oxytropidoceras packardi* zone at U.C.L.A. locality 2900.

Remarks.—*B. haydeni* (Gabb) is very close to the genotype, *B. beudanti* (Brogniart) as interpreted by Spath (1923, pl. 2, fig. 4a,b). It differs in having more closely spaced crescent-shaped ridges and a slightly more rounded venter. The specimens of *B. haydeni* (Gabb) found in the Cottonwood district of northern California are generally fragmental and often poorly preserved. In this state they may be confused with *Brewericeras hulenense* (Anderson), especially when the suture line is not preserved or the whorl section is crushed. An apparently consistent difference in the ornamentation of the umbilical wall of large specimens may be used to separate the two species when other criteria fail. The configuration of the growth lines across the umbilical wall of *Br. hulenense* is like that of a rounded chevron, inflected posteriorly across the inner half then anteriorly across the remainder of the wall. An indented spiral line is often present at the peak of this chevron. In *B. haydeni* the growth line is not inflected on the umbilical portion of the wall but is inflected anteriorly from the half-way mark to the umbilical edge.

Range.—*B. haydeni* (Gabb) has been found in association with the following

forms: *Oxytropidoceras packardi* Anderson, *Puzosia aldersona* Anderson, *Desmoceras* (*Pseudouhligella*) *vetus* Murphy and Rodda, and *Mortoniceras? hulenana* (Anderson).

Anderson has reported that this species occurs with *Brewericeras hulenense* (Anderson) (1938, p. 191). He also reports that the two species are abundant at Horsetown and Texas Springs (1938, p. 191; 1958, p. 212). No specimens of *Beudanticeras haydeni* have been recovered by the writers from these classic localities although *Brewericeras hulenense* is abundant at both places. Anderson's collections in the California Academy of Sciences from the above localities and from localities in his "Neptune zone" contain only one specimen (C.A.S. Type Coll. No. 5944) of *B. haydeni*. The specimen figured in his 1938 paper (pl. 48, figs. 2,3) is a small compressed specimen of *Brewericeras hulenense*. It is concluded, therefore, that the reported occurrences of *Beudanticeras haydeni* with *Brewericeras hulenense* in the "Neptune zone" of Anderson, at Horsetown and at Texas Springs are based largely on misidentifications and that the lowest occurrence of *B. haydeni* is in the *Oxytropidoceras packardi* zone of the middle Albian. The single exception, cited above, is from C.A.S. locality 1344, "Old Horsetown." Since there are cretaceous rocks of several ages ranging from lower Albian to Turonian in the vicinity of the site of Horsetown, (Rodda, 1960), we must wait for more positive proof that *B. haydeni* occurs with *Br. hulenense*.

The specimen figured in this paper (Pl. 105, figs. 1,2) was found in the lowest conglomerate of the Bald Hills formation on the North Fork of Cottonwood Creek by W. P. Popenoe of the University of California, Los Angeles.

Genus DESMOCERAS Zittel, 1884
Subgenus PSEUDOUHLIGELLA Matsumoto, 1942

In his discussions of the subgenus Matsumoto has distinguished two criteria by which *Pseudouhligella* may be distinguished from *Desmophyllites* Spath. The first of these is on the nature of the umbilicus: "Besides the typical *Desmoceras* (i.e. *latidorsella* Jacob), there are compressed forms which include the subgenus *Pseudouhligella* and the genus *Schlüteria* [=*Desmophyllites*].[1] Although these two resemble each other, *Schlüteria* has a very narrow, crater-like umbilicus, its sutural element U_{vi} being situated outside the umbilical shoulder, even at a comparative early stage of growth, whereas *Pseudouhligella* in the adult stage is gradumbilicate and is ornamented with a weak ventral subcosta." (Matsumoto, 1942, p. 25). The second criterion is on the basis of the number of elements in the suture: "*Desmophyllites*, which is one of the true desmoceratids, is allied to the present subgenus, but has more numerous elements in the suture-line, very narrow and crater-like umbilicus and, accordingly, a *Phylloceras*-like shell-form. No connecting form has yet been found between the Cenomanian *Pseudouhligella* and Campanian *Desmophyllites*." (Matsumoto, 1954, p. 252). According to

[1] [ ] are the writers'.

EXPLANATION OF PLATE 105

All figures ×1

FIGS. *1,2—Beudanticeras haydeni* (Gabb). *1*, lateral view of specimen 28659 U.C.L.A. Invert. Paleo. Cat. showing ornamentation; *2*, cross-sectional view of same specimen showing shape of whorl.

3—Brewericeras hulenense (Anderson). Specimen 28661 U.C.L.A. Invert. Paleo. Cat. figured here to show similarity of early whorls to early whorls of *Beudanticeras haydeni* (Gabb) with which it has been confused.

4,5—Puzosia sullivanae n. sp. Ventral and lateral views of the holotype, 28657 U.C.L.A. Invert. Paleo. Cat.

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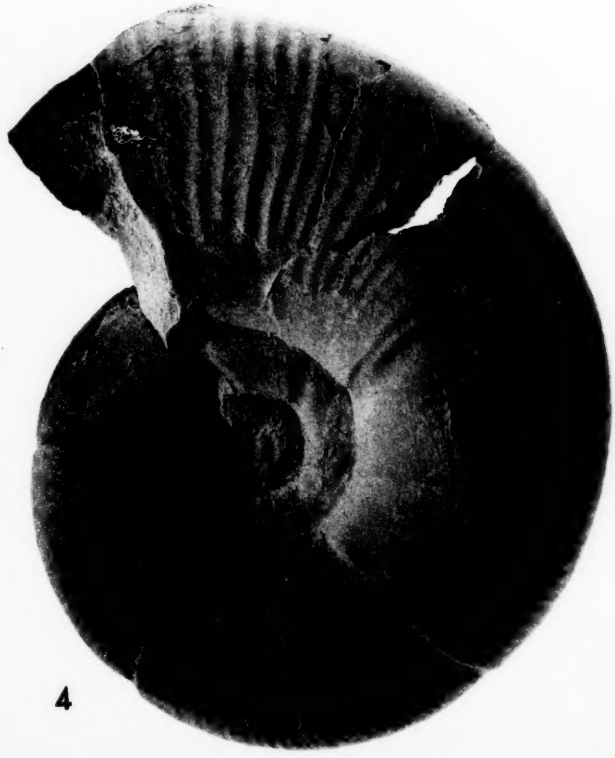

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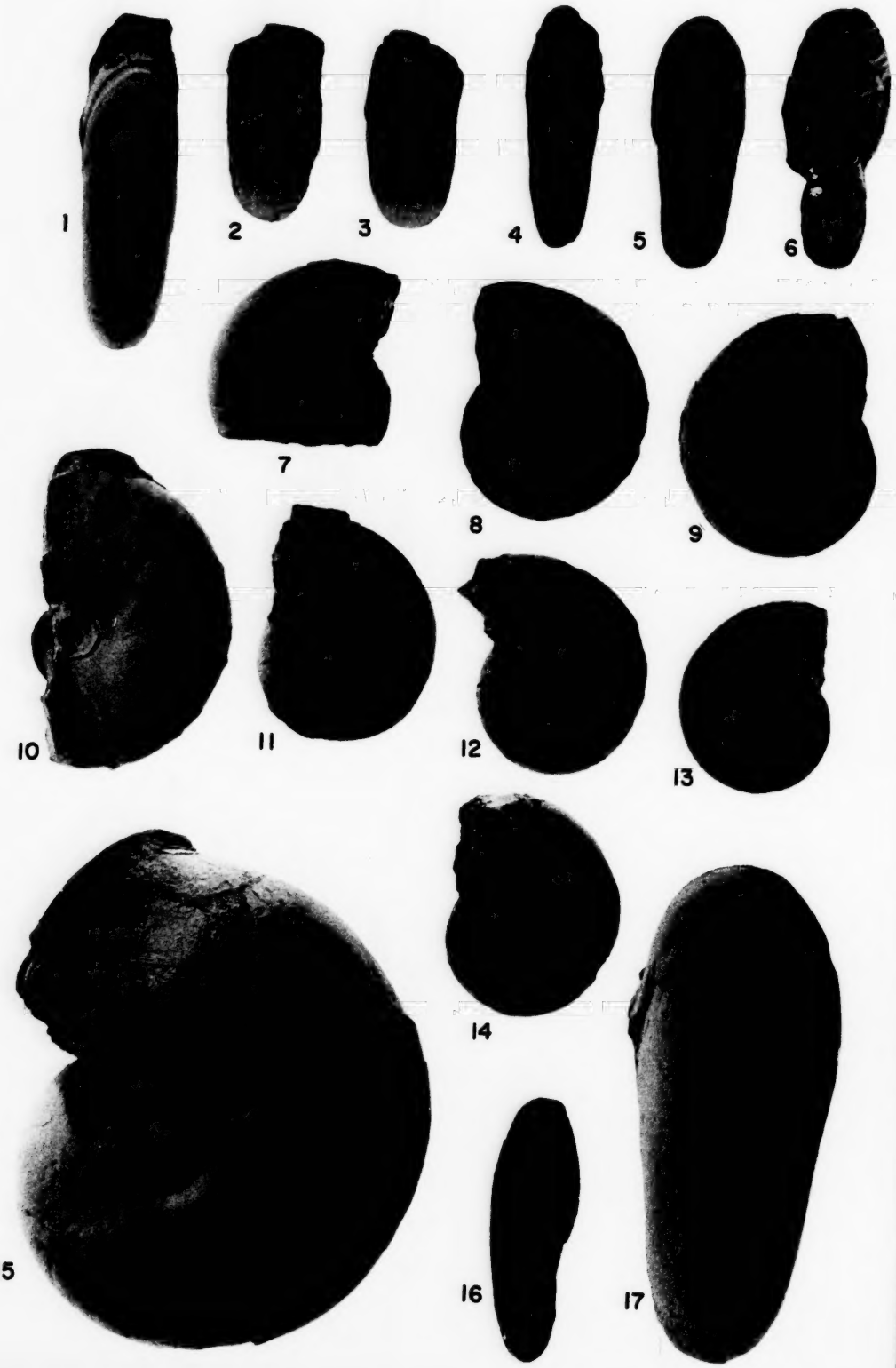
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Wright (1957, p. L370–71) *Pseudouhligella* ranges from upper Albian through Turonian while *Desmophyllites* is a Santonian-Campanian form.

The California forms from the Upper Albian and Cenomanian do not fit neatly into this classification. Most are not gradumbilicate (stair-step-like) and at least one, *Desmoceras barryae* Anderson, is very narrowly umbilicate. The suture lines of most species, however, have the same number of elements as the genotype of *Pseudouhligella*, *Desmoceras* (*Pseudouhligella*) *japonicum* Yabe. We have placed the California species in the subgenus *Pseudouhligella* Matsumoto, since the differences between them and the genotype are minor. We feel, however, that this group of species shows a very close relationship between the subgenus *Pseudouhligella* and the genus *Desmophyllites*, one that may not warrant generic or perhaps even subgeneric distinction.

In a recent paper, published 13 years after his death, F. M. Anderson (1958) described several species of *Pseudouhligella* which he assigned to the genera *Desmoceras* and *Beudanticeras*. Several dozen specimens collected by the authors and Willis P. Popenoe from the Bald Hills formation are assignable to one or the other of these species or are intermediate varieties. No attempt is made to revise the existing species as our collection does not have sufficient material to determine the variation of any of them.

DESMOCERAS (PSEUDOUHLIGELLA) sp. cf. D. (P.) BARRYAE Anderson

Pl. 106, figs. 1,4,5,6,7,8,10,12,13,14,16

Desmoceras (*Latisdorsella*) *barryae* Anderson, 1958, p. 21, pl. 12, figs. 2,2a.

Shell small to medium size, compressed, 80–90 percent involute; ornamentation consists of biconvex growth lines with peripheral ridges sometimes developed above the constrictions; constrictions on all specimens in later growth stages but variable in number (8–12 per whorl), width, depth and diameter at which they first appear on the shell; suture desmocerid, not retracted, with numerous auxillaries in the suspensive lobe; umbilical wall low, rounded.

Figured specimens.—The figured specimens are specimen numbers 28665, 28666, 28667, 28668, 28669, 28670, 28671, and 28672 U.C.L.A. Invert. Paleo. Cat.

Remarks.—This species occurs abundantly at a number of localities throughout the Bald Hills formation. It differs from *D.* (*P.*) *japonicum* in having a more rounded flank, in lacking the subangulate umbilical edge, and the first lateral lobe is more deeply incised than the ventral lobe, the reverse is true in *D.* (*P.*) *japonicum*. *D.* (*P.*) cf. *D*

EXPLANATION OF PLATE 106

All figures ×1

FIGS. *1,4–6,8–10,12–14,16—Desmoceras* (*Pseudouhligella*) cf. *D.* (*P.*) *barryae* Anderson. *1,10*. ventral and lateral views of specimen 28670 U.C.L.A. Invert. Paleo. Cat. showing constrictions of the body whorl; *4,12*, ventral and lateral views of specimen 28667 U.C.L.A. Invert. Paleo. Cat.; *5,6*, ventral and cross-sectional view of specimen 28665 U.C.L.A. Invert. Paleo. Cat., representing an inflated variety of the species; *8,12,14*, lateral views of specimens 28671, 28667, and 28665 U.C.L.A. Invert. Paleo. Cat., showing variation in development of constrictions in specimens of the same size; *9*, lateral view of specimen 28666 U.C.L.A. Invert. Paleo. Cat., representing the inflated variety; *13*, lateral view of small specimen, 28672 U.C.L.A. Invert. Paleo. Cat., showing narrow constrictions; *16*, cross-sectional view of specimen 28669 U.C.L.A. Invert. Paleo. Cat.

2,3,7,11—Desmoceras (*Pseudouhligella*) *japonicum* Yabe. *2,11*, ventral and lateral views of specimen 28663 U.C.L.A. Invert. Paleo. Cat.; *3,7*, ventral and lateral views of specimen 28662 U.C.L.A. Invert. Paleo. Cat.

15,17—Desmoceras (*Pseudouhligella*) cf. *D.* (*P.*) *argonauticum* (Anderson). Lateral and ventral views of specimen 28673 U.C.L.A. Invert. Paleo. Cat.

(*P.*) *barryae* differs from *D.* (*P.*) *ezoanum* Matsumoto and *D.* (*P.*) *poronaicum* (Yabe) in having frequent constrictions and from *D.* (*P.*) *vetus* Murphy and Rodda in having a narrower umbilicus.

DESMOCERAS (PSEUDOUHLIGELLA) sp. cf. D. (P.) ARGONAUTICUM (Anderson)
Pl. 106, figs. 15,17

Beaudanticeras argonauticum Anderson, 1958, p. 213, pl. 9, figs. 1,2.
Desmoceras (*Pseudouhligella*) *dawsoni* Whiteaves Matsumoto, 1958, p. 651.

Shell medium size, moderately inflated, about 80 percent involute; ornamentation of biconvex growth lines; constrictions biconvex, infrequent, not prominent; suture not retracted, with the first lateral lobe about as long as the ventral lobe; umbilical wall high, rounded at umbilical edge.

Figured specimen.—The figured specimen, specimen number 28673 U.C.L.A. Invert. Paleo. Cat., was collected with a number of smaller specimens at locality 3778.

Remarks.—*D.* (*P.*) cf. *D.* (*P.*) *argonauticum* differs from *D.* (*P.*) *alamoense* (Anderson) in having few, poorly developed constrictions and in being more inflated than the typical variety; from *D.* (*P.*) *vetus* Murphy and Rodda in having fewer constrictions, narrower and deeper umbilicus and in being more inflated; from *D.* (*P.*) *japonicum* in having fewer constrictions and a more rounded umbilical edge; from *D.* (*P.*) *ezoanum* Matsumoto in being more inflated and having rounded umbilical edge; from *D.* (*P.*) *barryae* in a larger umbilicus and more rounded whorl shape. Compared with *D.* (*P.*) *dawsoni* Whiteaves (1884, pl. 26, fig. 1; 1900, pl. 37, fig. 3) *D.* (*P.*) *argonauticum* has a narrower and deeper umbilicus, fewer and weaker constrictions, is more inflated, and has a broader venter.

The figured specimen of *D.* (*P.*) cf. *D.* (*P.*) *argonauticum* is considerably more inflated than the holotype (Anderson, 1958, pl. 9, figs. 1,2).

DESMOCERAS (PSEUDOUHLIGELLA) ALAMOENSE (Anderson)

Beaudanticeras alamoense Anderson, 1958, p. 213, pl. 5, figs. 2,2a.
Desmoceras (*Pseudouhligella*) *dawsoni* Whiteaves, Matsumoto, 1958, p. 651.

Shell medium size, moderately inflated, about 80 percent involute; ornamentation of biconvex growth lines; constrictions biconvex, frequent on larger specimens, preceded on the venter by a strong labial ridge; suture not retracted, with L about as long as E; umbilical wall low, rounded.

Remarks.—This species is very close to *D.* (*P.*) *argonauticum*, but may be eventually differentiated on the basis of whorl shape. It may also have a slightly higher stratigraphic position. *D.* (*P.*) *alamoense* also resembles *D.* (*P.*) *dawsoni* Whiteaves (1884, pl. 26, fig. 1; 1900, pl. 37, fig. 3), but has a more rounded whorl flank, and a broader venter.

DESMOCERAS (PSEUDOUHLIGELLA) JAPONICUM Yabe
Pl. 106, figs. 2,3,7,11

Desmoceras whiteavesi var. *japonicum* Yabe, 1904, p. 35, pl. 5, figs. 3,4.
Desmoceras (*Pseudouhligella*) *japonicum* Yabe, Matsumoto, 1938, p. 23, fig. 27; 1942, p. 26, fig. 1c; 1954, p. 252–257, pl. 18, figs. 1a,b.

Shell size small with a maximum diameter of 35 mm. for the California specimens collected to date. This size is much smaller than average for this species even though the body whorls of the specimens are preserved. At this size the shell is compressed; flanks flat and parallel; the umbilical edge is angulate, the umbilical wall steep and not rounded, abutting the previous whorl at right angles (i.e. the inner margins of whorls form perpendicular steps). Constrictions are infrequent up to a diameter of about 30 mm. Two closely spaced distinct constrictions are present on one specimen and the other shows very faint poorly developed but closely spaced constrictions in the last quarter turn of the body whorl indicating that larger specimens have the frequent biconcave constriction pattern characteristic of the species. Constrictions have a strong anterior inflection across the venter and are reflected in the external shell on the venter by a very shallow groove which lies just anterior to a labial ridge. Ornamentation consists of striae on the flanks with a tendency for subcostae to arise on the venter of the body whorl. Suture agrees in detail with that figured by Matsumoto (1954, p. 255, fig. 2(48)).

Holotype.—The holotype is from Japan.

Hypotypes.—The hypotypes are numbers 28662 and 28663 U.C.L.A. Invert. Paleo. Cat.

Remarks.—Several specimens of this species, including the hypotypes, were collected at locality 3478 near the top of the Bald Hills formation. The species is found in the uppermost Albian and Cenomanian in the Japanese Islands (Matsumoto, 1942, p. 28, fig. 2) and is most abundant in the middle and upper parts of the Cenomanian (Matsumoto, oral communication).

Genus EOGUNNARITES Wright and Matsumoto, 1954

EOGUNNARITES MATSUMOTOI n. sp.

Pl. 104, figs. 1,2,3

The shell is small with a maximum measured diameter of approximately 50 mm.; number of whorls 5 or 6; whorl cross-section depressed up to 30 mm. diameter and probably thereafter but the later part of the whorl is crushed; ornamentation of primary and secondary ribs; primary ribs sharp-crested, narrow, more or less straight, extending from the umbilical edge across the flank, branch ventro-laterally into two rounded ribs of equal size, other rounded ribs intercalated on the peripheral half of the penultimate whorl but all the observed ribs on the peripheral half of the body whorl are pairs that branch from the flank ribs; six prominent prosiradiate constrictions present on the penultimate whorl; constrictions not detected on the body whorl but this part of the specimen is very fragmentary; constrictions more prosiradiate than ribs and truncate the secondary ribs they intersect; suture line very close to that of *E. unicus* (Yabe) as figured by Wright and Matsumoto (1954, p. 127, fig. 20c).

Holotype.—The holotype is number 28664 U.C.L.A. Invert. Paleo. Cat. Its dimensions are:

Diameter	Height	Width	Umbilicus
29 mm.	12 mm.	15 mm.	8½ mm.
21 mm.	9 mm.	11 mm.	6 mm.
8 mm.	3.7 mm.	4.5 mm.	2 mm.

The holotype was found at U.C.L.A. locality 3775 in the first conglomerate bed in the sequence of the Bald Hills formation on the North Fork of Cottonwood Creek.

Remarks.—*E. matsumotoi* n. sp. differs from *E. unicus* (Yabe), the genotype, in having elongate, sharp-crested ribs from which the secondary ribs arise instead of tubercles. The ribs on the body whorl are not intercalated as they are on *E. unicus*. *E. matsumotoi* n. sp. differs from an undescribed species of *Eogunnarites*, which occurs above the Bald Hills formation, in being more depressed, having the ribs branch high on the flank into two rather than arising in bundles of three or four from weak umbilical bullae as in the undescribed form.

This is the first record of this genus in America.

The species is named for T. Matsumoto, Kyushu University, Japan.

Family BRANCOCERATIDAE Spath, 1933

Genus MORTONICERAS Meek, 1876

MORTONICERAS GAINESANA (Anderson)

Pl. 103, fig. 8

Pervinquieria gainesana Anderson, 1958, p. 257, pl. 4, fig. 1,1a.

Pervinquieria sylvana Anderson, 1958, p. 258, pl. 4, fig. 2,3; pl. 7, fig. 2.

Pervinquieria tehamaensis (Reagan), Anderson, 1958, p. 257, pl. 3, fig. 1.

Pervinguieria aff. *P. inflata* Sowerby, Anderson, 1958, p. 258, pl. 7, fig. 3.

Shell large with a maximum measured diameter of 420 mm.; whorl cross section quadrate up to about 250 mm. diameter after which the whorl section becomes progressively more ovate; ribs single on the body whorl but branching from umbilical bullae in penultimate whorl, lateral tubercles slightly above the midpoint of the flank; ribs radiate to slightly prosiradiate; venterolateral tubercles prominent on later whorls, but reduced in earlier whorls to inflated ribs with numerous small clavate ridges superimposed.

Types.—The holotype is specimen number 14940 in the University of California, Berkeley, Department of Paleontology type collection.

The hypotype, specimen number 28674 U.C.L.A. Invert. Paleo. Cat., was collected at locality number 3775. Dimensions: at 420 mm. diameter, height of whorl 100 mm., width of whorl 85 mm. (interrib), 115 mm. (including ribs), umbilicus 244 mm.

Remarks.—This species differs from *M.*

hulenana (Anderson) in the slightly more prominently developed lateral tubercle and the branching ribs on the penultimate whorl. *M. gainesana* differs from *M. tehamaensis* (Reagan) in having bifurcating ribs, less prominent lateral tubercles, and a more quadrate cross-section.

All specimens of this species in our collection came from nodular limestone clasts in the lowest conglomerate unit of the Bald Hills formation exposed on the North Fork of Cottonwood Creek, Shasta County, California. Their true stratigraphic position is not known in this district.

FOSSIL LOCALITIES

All numbers refer to localities described in the invertebrate paleontology locality catalogue, University of California, Los Angeles. With the exception of locality 3287 all localities are in the Ono quadrangle, Shasta County, California, With the exceptions of localities 3287, 3816 and 3817, all localities are in the Bald Hills formation.

2901 Huling Creek. At narrows in stream about 150 yards upstream from its mouth in the lowest conglomerate of the Bald Hills formation. 2000′ S and 800′ W of the NE corner sec. 17, T30N, R6W.

3287 Millville quadrangle, Shasta Co., California. Massive sandstone in the bed of Salt Creek, about 575′ N and 700′ E of SW corner sec. 26-33N-3W. Near base of Member I.

3464 Conglomerate bed in small gully about 150′ W of the Gas Point road. 1600′ E and 1900′ S of the NW corner sec. 16-30N-6W.

3465 Conglomerate bed on ridge on E side of the North Fork of Cottonwood Creek. 700′ E and 2200′ N of SW corner sec. 16-30N-6W.

3466 In same gully as 3464, but 1000′ NW (Upstream). Limestone nodule in sandy mudstone.

3467 North side of the North Fork of Cottonwood Creek, about 1000′ WSW from the mouth of Huling Creek. Lowest conglomerate of the Bald Hills formation. 2500′ N and 1450′ W of the SE corner sec. 17-30N-6W.

3469 East bank of the North Fork of Cottonwood Creek, about 1700′ S 50° E from the mouth of Huling Creek. Sandy conglomerate. 700′ E and 1900′ N of the SW corner sec. 16-30N-6W.

3470 Beside irrigation ditch along E side of the North Fork of Cottonwood Creek. Conglomerate. 1250′ N and 715′ E of the SW corner sec. 16-30N-6W.

3471 Tributary of the North Fork of Cottonwood Creek. Limestone nodules in mudstone. 1000′ S and 1100′ E of the NW corner sec. 20-30N-6W.

3472 Tributary of the North Fork of Cottonwood Creek, about 800′ ENE from locality 3471. Massive graywacke bed. 1000′ S and 2000′ E of the NW corner sec. 20-30N-6W.

3474 Coyote Creek. Thick, massive graywacke bed. 2000′ S of the NW corner sec. 30-30N-6W.

3476 Coyote Creek, about 1700′ ESE from locality 3474. Massive graywacke. 1600′ E and 2300′ S of NW corner sec. 30-30-N-6W.

3477 Coyote Creek, about 1000′ E from locality 3476. Massive graywacke. 2400′ W. and 2800′ N of SE corner sec. 30-30N-6W.

3478 Coyote Creek, about 400′ SE of locality 3477. Massive graywacke. 2450′ N and 1950′ W of the SE corner sec. 30-30N-6W.

3762 Tributary of the North Fork of Cottonwood Creek in a very small gully on the north bank of the creek. Limy graywacke nodules in siltstone. 900′ S and 2650′ W of the NE corner sec. 30-30 N-6W.

3763 Tributary of the North Fork of Cottonwood Creek, about 350′ ESE from locality 3762. Conglomerate. 1000′ S and 2200′ W of the NE corner sec. 30-30N-6W.

3764 North Fork of Cottonwood Creek just below the mouth of Huling Creek. Massive graywacke. 2500′ S and 700′ W of the NE corner sec. 17-30N-6W.

3765 West bank of the North Fork of Cottonwood Creek. Conglomeratic graywacke. 1600′ N and 550′ E of the SW corner sec. 16-30 N-6W.

3766 Same gully as locality 3466, but about 300′ NW Concretionary graywacke. 800′ S and 800′ E of the NW corner sec. 16-30N-6W.

3767 About 100′ above the mouth of a small gully on the E side of tributary of the North Fork of Cottonwood Creek Limy, conglomeratic graywacke. 1900′ S and 2200′ E of the NW corner sec. 16-30N-6W.

3768 Tributary of the North Fork of Cottonwood Creek, about 400′ NW from locality 3767. Conglomeratic graywacke. 1550′ S and 2000′ E of the NW corner sec. 16-30N-6W.

3769 In small E-W canyon about 750′ E of the Gas Point road. Massive graywacke. 1550′ S and 2600′ E of the NW corner sec. 16-30N-6W.

3771 In small gully on the N side of the canyon of locality 3769. Limestone nodules in siltstone. 900′ S and 2600′ W of the NE corner sec. 16-30N-6W.

3775 North bank of the North Fork of Cottonwood Creek. In second conglomerate bed above the base of the Bald Hills formation and about 10 feet stratigraphically above locality 3467.

3776 North bank of the North Fork of Cottonwood Creek, and about 25–30′ strati-

graphically above locality 3775. Limestone nodules in pebbly mudstone.

3777 Lowest conglomerate of the Bald Hills formation exposed amongst placer gravels on stream terrace about 600′ NW of the junction of Huling Creek and the North Fork of Cottonwood Creek.

3778 Huling Creek. About 5′ stratigraphically above the top of the basal conglomerate of the Bald Hills formation (locality 2901). Limestone nodules in mudstone 2050′ S and 750′ W of the NE corner sec. 17-30N-6W.

3808 Roaring River. Mudstone on N bank. 3500′ E and 3000′ N of the SW corner of sec. 1-29N-7W.

3816 Coyote Creek, about 1300′ SSE from locality 3478. Thin limestone bed in mudstone of an unnamed formation above the Bald Hills formation. 750′ W and 2400′ N of the SE corner sec. 30-30N-6W.

3817 Tributary of the North Fork of Cottonwood Creek about 4800′ ESE of locality 3763, beside road to old ranch house. Limestone pebble conglomerate, and limestone nodules in mudstone. 2500′ E and 1800′ S of the NW corner sec. 29-30N-6W.

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(*Explanation of* PLATE 107 *on next page.*)

EXPLANATION OF PLATE 107

FIGS. *1–3*—*Pseudhelicoceras petersoni* (Anderson, *1,2*, oblique and lateral views showing ornamentation; *3*, suture line, ×1

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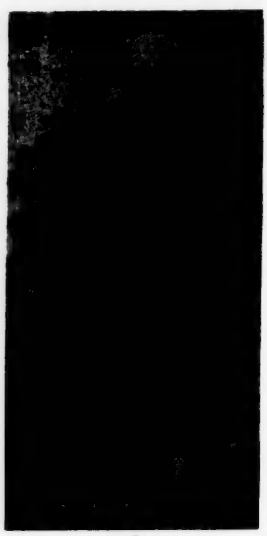

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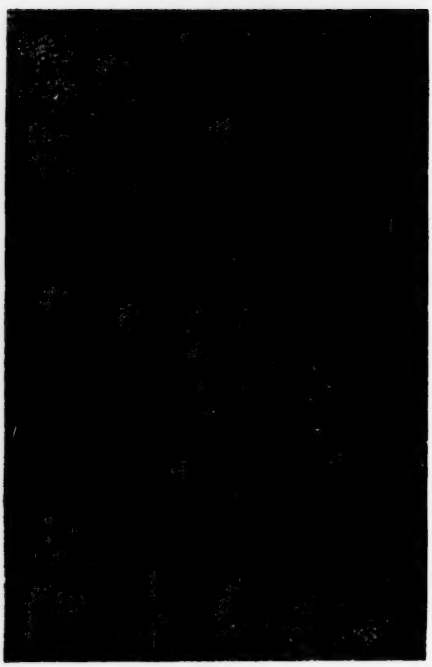

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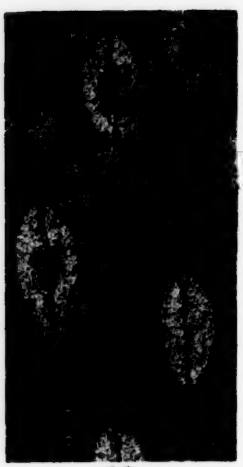

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JOURNAL OF PALEONTOLOGY, V. 34, NO. 5, P. 859–861, PL. 108, SEPTEMBER, 1960

RE-EVALUATION OF THE TYPE SPECIES OF *ARTHROPORA* ULRICH

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ABSTRACT—Syntypes of *Arthropora shafferi* (Meek), the type species of *Arthropora*, are found to belong to the genus *Graptodictya*. Thus *Arthropora* is a synonym of *Graptodictya*.

INTRODUCTION

THROUGH the decades many authors have described bryozoan species and genera which have remained in the original geological reports to be used or discussed only infrequently in the years since. One reason for this plight is that the inadequacy of many of the original descriptions and illustrations has prevented later workers from being able to recognize them. These species (particularly the type species) require revision in the light of present day bryozoan systematics and techniques. When such a revision is, in part, achieved bryozoan workers shall have useful data to interpret critically the stratigraphic significance and phylogenetic relations of this interesting group of colonial animals. This redescription of *Arthropora shafferi* (Meek) from type material is part of a continuing program in the study and revision of Paleozoic Bryozoa.

The writer is indebted to Professor K. E. Caster, University of Cincinnati, who arranged the loan of Meek's specimens.

SYSTEMATIC DESCRIPTION

Order CRYPTOSTOMATA
Genus GRAPTODICTYA Ulrich 1882

Graptodictya Ulrich 1882, p. 165.
Arthropora Ulrich 1882, p. 167.
Type species (designated by Ulrich, 1882, p. 165)—*Ptilodictya perelegans* Ulrich, 1878, p. 94, pl. 4, figs. 16,16a.

GRAPTODICTYA SHAFFERI (Meek) 1872
Pl. 108, figs. 1–11

Ptilodictya (*Stictopora*) *shafferi* Meek 1872, Proc. Acad. Nat. Sci. Phila. (February, 1872), p. 317, not figured.
Ptilodictya (*Stictopora*) *shafferi* Meek, Meek, 1873, Ohio Geol. Survey, v. 1, pt. 2, p. 69,70, pl. 5, figs. 1a,b,c.
Arthropora shafferi Meek, Ulrich, 1882, Jour. Cincinnati Soc. Nat. Hist., v. 5, p. 167, pl. 7, figs. 10,10a.

Type Material.—Lectotype, University of Cincinnati Museum 3789-a, colony 6×6×3 cm. enclosed in calcilutite. Syntypes UCM 3789-b,c,d, are three additional blocks of calcilutite in which fragments of *Grapto-*

EXPLANATION OF PLATE 108

FIGS. *1–11.*—*Graptodictya shafferi* (Meek). *1*—Tangential section cut from lectotype UCM 3789-a showing well-defined zooecial openings and pustulate rows on the surface of the zooecial walls, ×50; *2–5*, YPM, 20796, 20799, 20797, 20798, respectively; typical small fragments with side branches broken off, ×5; *6*, transverse section cut from lectotype UCM 3789-a showing a slender mesotheca without median tubuli, ×50; 7, YPM 20800, zoarial fragment showing fine striae on lateral margins and on zooecial walls, ×15; 8, portion of the lectotype UCM 3789-a showing undulating fragments of the colony enclosed in calcilucite, ×5; *9*, deep tangential section cut from lectotype UCM 3789-a showing thin zooecial walls which thicken towards periphery, ×50; *10*, shallow tangential section cut from lectotype UCM 3789-a showing pustulate rows in the zooecial walls, ×100; *11*, oblique longitudinal section cut from lectotype UCM 3789-a. Typical section of undulating branch of colony, ×50.

dictya shafferi are abundant. The locality as given by Meek to whom the material was originally loaned follows: "Toward the lower part of the Cincinnati group of the Lower Silurian, at Cincinnati, Ohio." Chappars (1936, p. 5) located the syntypes as "Maysville—(Bellevue, Corryville) (Ord.). Cincinnati. Ohio."

Additional Material.—Yale Peabody Museum 20796 to 20800, Liberty formation, Four Mile Creek, seven miles north of Oxford, Ohio; Ordovician. Collected by Dr. W. M. Shideler.

Description.—Zoaria are very slender ribbon-shaped bifoliate branches (pl. 108, figs. 2–4,7,8). In most colonies the branches grow along the main stems from which new stems fork. No single main stem has continued growth in a direct line so that well developed colonies, such as UCM 3789-a, have spreading and successively dividing stems and branches. The delicate colonies are readily fragmented by the weight of enclosing sediment. In fragments, commonly up to 2.0 cm. in length, the side branches are generally broken off near their junction with the main stem so that many specimens have the erroneous appearance of strongly barbed sticks. The very narrow lateral margins of the branches and stems lack zooecia and are marked with fine striae (pl. 108, fig. 7).

The zooecial openings are well-defined by a fine circular ridge and striae are present on the surface of the zooecial walls. Mesopores and acanthopores are absent (pl. 108, figs. 1,7).

Few zooecial structures are present in the very slender branches. Zooecial walls leave the mesothecal plane at an angle of 20 to 30 degrees and continue in this direction for most of their growth. Near the periphery the walls suddenly thicken and turn to open directly at the zooecial surface. The walls are thin partitions except for the narrow peripheral region where they thicken and have lamellate wall structure.

The bilaminate mesotheca lacks median tubuli (pl. 108, fig. 6).

Short lamellate superior hemisepta have not been observed at the base of the thickening walls. The fine striations on the external zooecial walls appear as very shallow pustulate rows in the wall lamellae.

Remarks.—Ulrich (1882, p. 167) mistakenly identified the finely broken branches as jointed structures and erected the genus *Arthropora*, designating *Graptodictya shafferi* as the type species, primarily upon this erroneous observation.

The arrangement and outline of the zooecial openings, the orientation of the zooecial tubes, zooecial wall structure, simple, slender mesotheca, and absence of median tubuli, acanthopores, and mesopores identify this bifoliate species as belonging to the genus *Graptodictya* Ulrich (Phillips, 1960).

In comparison to *Graptodictya perelegans* (Ulrich) and *G. elegantula* (Hall), *G. shafferi* has more slender branches with more frequent successive branching of the stems, narrower lateral margins, distinctly different abundance of zooecia (longitudinally and laterally). It is similar to these two species in the zooecial wall structure and the

MEASUREMENTS

	Lectotype UCM 3789-a	
	Minimum mm.	Maximum mm.
Zoarial branch width	0.64	1.3
Zoarial branch depth	0.24	0.3
Ranges on branch	7	11
No. of zooecia/2 mm.		
Longitudinally	4	8
Laterally	10	10
Longitudinal interspace	0.14	0.20
Lateral interspace	0.06	0.12
Zooecial openings	(0.06×0.12)	(0.12×0.18)
Ratio: $\frac{\text{Width of mature region of zooecium}}{\text{Width of zooecium}}$	0.33	

presence of striations on the external surface of the zooecial walls and narrow lateral margins.

The specimen illustrated by Meek (1873, pl. 5, fig. 1) was not found among the syntypes in the collections of the University of Cincinnati Museum.

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JOURNAL OF PALEONTOLOGY, V. 34, NO. 5, P. 862–873, PLS. 109–112, 1 TEXT-FIG., SEPTEMBER, 1960

FOSSILS FROM THE JOHNSON SPRING FORMATION, MIDDLE ORDOVICIAN, INDEPENDENCE QUADRANGLE, CALIFORNIA

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ABSTRACT—Interbedded Middle Ordovician quartzite and carbonate rocks of the Independence Quadrangle Inyo Mountains, California are here named the Johnson Spring formation. Correlation with the Eureka quartzite of the Great Basin is based on lithologic similarity and stratigraphic position. The carbonate rocks of the Johnson Spring formation contain a large fauna in which corals are predominent. New species are *Anthaspidella inyoensis* (sponge); *Streptelasma tennysoni, Paleophyllum mazourkensis, Grewingkia whitei, Brachyelasma bassleri, Lichenaria sisyphi, Eofletcheria kearsargensis*, (corals); *Ptychopleurella arthuri*, (brachiopod). These and other fossils occurring in the Johnson Spring formation indicate a Trentonian (?) age.

INTRODUCTION

GENERAL lack of paleontologic data from the Eureka group makes the fossils of the Johnson Spring formation important in the dating of these rocks. Furthermore the largly unknown nature of westernmost Middle Ordovician faunas, and the fact that the Johnson Spring formation contains the only fossiliferous rock related to the upper part of the Eureka group renders the rocks and fossils described in this paper doubly interesting.

The early summer of 1958 was spent in geologic mapping and fossil collecting in the Johnson Spring formation in the eastern half of the U. S. Geological Survey Independence Quadrangle, California, 15 minute series. Here the most prominent geographic feature is Mazourka Canyon which runs in a north-south direction and bisects the eastern half of the quadrangle (see text-fig. 1).

I wish to thank Dr. R. L. Langenheim, Jr. who suggested the problem, led a reconnaissance of the area, and provided valuable help by reading and criticizing the manuscript. Thanks are also due to Dr. J. W. Durham who read and criticized the manuscript, to J. L. Greife and R. W. Nelson Jr. for help with the field mapping, and to Mr. Owen Poe for help in preparation of text-fig. 1. Field work was partially financed by funds made available by the Department of Paleontology of the University of California at Berkeley.

JOHNSON SPRING FORMATION

Description.—The name Johnson Spring formation is here proposed for interbedded limestone, dolomite, and quartzite that has previously been referred to as Undifferentiated Upper Part of the Eureka Group (Langenheim, *et al.*, 1956, p. 2092). Outcrops of this formation parallel outcrops of other Paleozoic formations along the eastern side of Mazourka Canyon (text-fig. 1). This formation also crops out in the syncline south of the entrance to Mazourka Canyon. The Johnson Spring formation conformably overlies the Barrel Spring formation and conformably underlies the Ely Springs dolomite and may be defined as the interbedded carbonate rocks and quartzites that lie between these two formations.

The thickness of the Johnson Spring formation ranges from 163 feet to 384 feet in the Independence Quadrangle. Langenheim, *et al.* (1956) described six stratigraphic sections of this formation. The two most abundantly fossiliferous sections are shown in text-fig. 1. The northernmost section is 208 feet thick and is called the Lead Canyon Trail section (Langenheim, *et al.*, 1956, p. 2092). Directly south of this section is the First South section which is 163 feet thick (Langenheim, *et al.*, 1956, p. 2092).

The Lead Canyon Trail section is here designated the type section of the Johnson Spring formation. This section contains the following units (modified after Langenheim, *et al.*, 1956, p. 2086).

ELY SPRINGS DOLOMITE

JOHNSON SPRING FORMATION

16. Quartzite, medium-grained, white, weathering white to buff, vitreous.... 20′
15. Dolomite, fine-grained, gray, weathering gray, beds up to 6 inches thick, containing flint nodules..... 14′
14. Limestone, medium-grained, black, weathering dark gray to black, beds

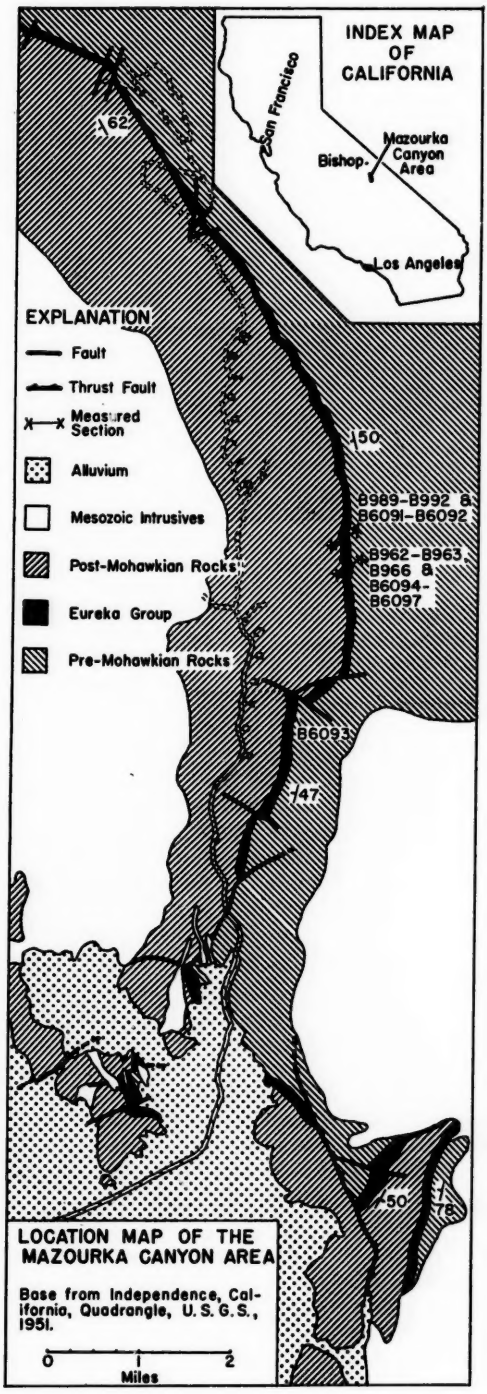
about 3 inches thick with flint nodules and siliceous fossils	22′
13. Limestone, medium-grained, black, mottled with gray dolomite, beds 3 inches thick with siliceous fossils	8.5′
12. Interbedded limestone, shale, siltstone, and quartzite, gray, weathering gray, beds 3 inches to 1 inch thick	9.5′
11. Covered, limestone and siltstone similar to unit 12	14′
10. Quartzite, medium-grained, white, weathering white, massive, shattered and recemented	23′
9. Limestone, medium-grained, dark gray, weathering gray, sandy, irregular bedding	27′
8. Quartzite, medium-grained, white, weathering buff	6′
7. Quartzitic siltstone, white, weathering buff, thin bedded	3.5′
6. Interbedded siltstone and sandstone, buff	5.5′
5. Covered	8.5′
4. Sandstone, white, weathering buff, calcareous	6′
3. Sandstone, gray, weathering olive-buff	4.5′
2. Quartzitic siltstone, similar to unit 7.	5′
1. Quartzite, medium-grained, white, weathering buff, massive, shattered and recemented	31′
	208′

BARREL SPRING FORMATION

This sequence of an upper and basal quartzite separated by interbedded carbonate rocks, sandstones, and quartzites occurs in the central part of the Mazourka Canyon area. To the north the middle beds are less clastic and to the south detrital rocks become more pronounced. This southward increase in the proportion of detrital rocks continues beyond the Independence Quadrangle. In the New York Butte Quadrangle and the Darwin Quadrangle over 400 feet of quartzite is reported and carbonate rocks are absent (Merriam and Hall, 1957, p. 4; and Hall and Mackevett, 1958, p. 7).

Age.—In the Mazourka Canyon area the following fossils have been collected from the Johnson Spring formation by Langenheim, *et al.* (1956, p. 2093) and this author.

SPONGES
Anthaspidella inyoensis n. sp.
CORALS
**Lambeophyllum sp. cf. L. profundum* (Conrad)
Streptelasma sp. 1
Streptelasma sp. 2
Streptelasma sp. 3
Streptelasma sp. cf. S. distinctum Wilson
Streptelasma sp. cf. S. prolongatum Wilson
Streptelasma tennysoni n. sp.
**Streptelasma sp.*



TEXT-FIG. *1*—Location map of the Mazourak Canyon area, California.

Paleophyllum mazourkensis n. sp.
Paleophyllum rugosum Billings
Coelostylis (?) *sp.*
Grewingkia whitei n. sp.
Brachyelasma bassleri n. sp.
Brachyelasma (?) *sp.*
Lichenaria (?) *sp. cf. L. heroensis* (Raymond)
Lichenaria sisyphi n. sp.
Lichenaria sp.
Eofletcheria kearsargensis n. sp.
BRYOZOANS
Hallopora sp. cf. H. tolli Bassler
BRACHIOPODS
Lingula sp.
Lingulasma (?) *sp.*
**Glyptorthis* (?) *sp.*
**Hebertella* (?) *sp.*
Ptychopeleurella arthuri n. sp.
**Resserella* (?) *sp.*
**Sowerbyella sp. cf. S. punctostriata* Mather
PELECYPODS
**Ctenodonta sp. cf. C. nasuta* (Hall)
GASTROPODS
**Hormotoma sp. cf. H. gracilis* Hall
**Hormotoma* (?) *sp.*
**Lophospira sp.*
**Maclurites* (?) *sp.*
**Raphistomina sp.*
Subulites (?) *sp.*
**Trochonema sp. cf. T. beloitense* Whitfield
CEPHALOPODS
**Ehlersoceras sp.*
ANNELIDS
Oenonites (?) *sp.*
Scolithus sp.

* Indicates species identified by Langenheim *et al.* (1956, p. 2093).

These fossils have a general Blackriveran-Trentonian aspect with the ranges of most of the genera overlapping in the Trentonian. The corals *Grewingkia* and *Brachyelasma* have previously been reported as occuring only in post-Trentonian rocks. These genera, especially *Brachyelasma*, are not well known and if the North American species of *Streptelasma* were critically reviewed many would undoubtedly be reassigned to either *Grewingkia* or *Brachyelasma*. Therefore if the Johnson Spring formation is considered older than Trentonian the ranges of five genera must be extended (*i.e. Anthaspidella, Lambeophyllum, Coelostylis, Lichenaria, Eofletcheria*); if on the other hand it is Trentonian or younger the ranges of only two genera would be extended (*i.e. Grewingkia* and *Brachyelasma*). Thus taking into account the overlap and necessary extensions of generic ranges, the age of the formation appears to be Trentonian.

CORRELATION

Lithology and stratigraphic position are the only means of correlating the Johnson Spring formation with the Eureka quartzite of other areas. The fauna of the Mazourka Canyon area cannot be used because in other areas the Eureka quartzite is unfossiliferous. Langenheim *et al.* (1956, p. 2094) correlate the underlying Barrel Spring formation with McAllister's unit 1 of the Eureka quartzite in the Quartz Spring area, California. Langenheim's Undifferentiated Upper Part of the Eureka group, the Johnson Spring formation, is correlated with McAllister's unit 2 of the Eureka quartzite (McAllister, 1952, p. 12). If these correlations are accepted it becomes convenient to consider the Barrel Spring formation and the Johnson Spring formation as parts of a group. A similar bi-partite subdivision of the Eureka quartzite occurs elsewhere in California and Nevada. In the Darwin Quadrangle, California, the basal quartzite is platy and weathers brown (Hall and Mackevett, 1958, p. 7), at Eureka, Nevada, it is silty and weathers brown (Kirk 1933, p. 28; Nolan, Merriam, and Williams, 1956, p. 30), and in the Antelope and Monitor Ranges, Nevada, it is replaced by fossiliferous shale (Kirk, 1933, p. 28 and p. 32; Merriam and Anderson, 1942, p. 1685; Nolan, Merriam, and Williams, 1956, p. 30). Webb (1958, p. 2341) redefined the Eureka quartzite at Lone Mountain, Nevada, and placed the lower unit in the Copenhagen formation. At Lone Mountain the uppermost Copenhagen formation consists of sandy dolomite, and the lowermost Eureka quartzite consists of yellowish to reddish-brown sandstone (Webb, 1958, p. 2341). I consider these last two units correlative with the Barrel Spring formation (lower Eureka group) of the Mazourka Canyon area.

SYSTEMATIC DESCRIPTIONS

Phylum PORIFERA Grant, 1872
Class DEMOSPONGIA Sollas, 1875
Order LITHISTIDA Schmidt, 1870
Suborder ANOMOCLADINA Zittel, 1878
Family EOSPONGIIDAE de Laubenfels, 1955
Genus ANTHASPIDELLA Miller, 1889

ANTHASPIDELLA INYOENSIS n. sp.

Pl. 109, fig. 7

Anthaspidella cf. A. scutula Ulrich and Everett, Langenheim, *et al.*, 1956, p. 2093.

Description.—Diameter up to 146 mm.;

saucer shaped, shallow; stem turbinate, short; basal surface concave and shallow; oscules numerous, 5 mm. to 17 mm. apart; oscules spaced closer toward center, peripherally further apart and elongated; 13 to 28 radiating furrows around oscules, merging freely between oscules; parallel canals extend from furrows through sponge; megascleres forming irregular polygonal network in interior.

Remarks.—Poor preservation and recrystalization obscures the canal system and prevents a more detailed description of the sponge interior. Externally *A. inyoensis* resembles *A. scutula* Ulrich & Everett (1890, p. 261), but the concentrically wrinkled base, wider spaced oscules, and more numerous oscular furrows distinguish it from the latter species. *A. inyoensis* is abundant and everywhere occurs in the same rock unit, but stratigraphically below the characteristic tetracorals of the Johnson Spring formation.

The specific name was derived from the name of the Inyo Mountains.

Occurrence.—B6091, B963, Johnson Spring formation, Independence Quadrangle, California.

Types.—Holotype number 37694, deposited in the Museum of Paleontology of the University of California, Berkeley, California.

Phylum COELENTERATA Frey & Leuchart, 1847
Class ANTHOZOA Ehrenberg, 1843
Order RUGOSA Milne-Edwards & Haime, 1850
Suborder STREPTELASMATINA Wedekind, 1927
Superfamily CYATHAXONIICAE Milne-Edwards & Haime, 1850
Family METRIOPHYLLIDAE Hill, 1939
Genus LAMBEOPHYLLUM Okulitch, 1938

LAMBEOPHYLLUM sp. cf. L. PROFUNDUM (Conrad)
Pl. 109, fig. 3,4

Lambeophyllum cf. L. profundum (Conrad), Langenheim *et al.*, 1956, p. 2093.

Description.—Solitary, trochoid, 5 mm. to 8 mm. long; oval, 6 mm. by 8 mm. to 8 mm. by 12 mm.; septa arranged in quadrants, 29 to 38 septa; minor septa very short, appearing as ridges between major septa in upper part of calyx; cardinal septum elongate and straight; septa in cardinal quadrants bent away from cardinal septum, in counter quadrants bent toward counter septum; major septa joined, those nearest cardinal or alar septa join closer to periphery because of greater septal bending; calyx deep, about $\frac{1}{2}$ the corallum height.

Remarks.—This coral resembles *L. profundum* (Conrad) (1853, p. 335) in most characters, but differs in having greater lateral expansion during growth. The specimens were too fragile for sectioning; therefore no horizontal structures were seen. Two specimens were available for study.

Occurrence.—B991, Johnson Spring formation, Independence Quadrangle, California.

Types.—Hypotype numbers 37695 and 37696, deposited in the Museum of Paleontology of the University of California, Berkeley, California.

Superfamily ZAPHRENTICAE Milne-Edwards & Haime, 1850
Family STREPTELASMATIDAE Nicholson, 1889
Subfamily STREPTELASMATINAE Nicholson, 1889
Genus STREPTELASMA Hall, 1847

STREPTELASMA SP.1

Streptelasma sp., Langenheim, *et al.*, 1956, p. 2093, in part.

Description.—Solitary, trochoid, basal tips and calicular edges broken; 10 mm. to 27 mm. in length, diameter 10 mm. to 13 mm.; minor septa absent or obscured in stereozone; major septa long, extend $\frac{3}{4}$ of the distance to the center, wavy, 0.8 mm. to 0.2 mm. thick, dilate uniformily toward periphery; 32 to 43 major septa; stereozone well developed, 1 mm. to 1.5 mm. thick.

Remarks.—Recrystalization has destroyed features necessary for positive specific identification. The apparent absence of minor septa distinguishes this form from the other species of *Streptelasma* in the area. Three specimens were available for study.

Occurrence.—B963, B6091, B6094, Johnson Spring formation, Independence Quadrangle, California.

STREPTELASMA SP. 2

Description.—Solitary, trochoid, base and calicular edge broken; 11 mm. long, diameter 10 mm.; calyx 5 mm. deep; 76 alternat-

ing major and minor septa; major septa extend ¾ of the distance to the center, straight to wavy, dilated near periphery; cardinal septum prominent and elongate; septa on either side of cardinal septum bend outward and join adjacent septa; an irregular axial structure is present.

Remarks.—The specimen was too fragile for sectioning. Its prominent and elongate cardinal septum distinguishes it from the other species of the genus in the area. One specimen was available for study.

Occurrence.—B6095, Johnson Spring formation, Independence Quadrangle, California.

Streptelasma sp. 3

Description.—Solitary, trochoid; 18 mm. to 22 mm. long, 13 mm. to 17 mm. in maximum diameter; circular to oval in section; major and minor septa alternating; 35 to 45 major septa, extend ¾ of the distance to the center, straight to wavy; septa dilate peripherally; narrow irregular axial structure present.

Remarks.—All specimens were too poorly preserved to permit specific identification. These differ, from other local species of *Streptelasma*, in having major and minor septa and in lacking a prominent cardinal septum. Three specimens were available for study.

Occurrence.—B6091, B6095, Johnson Spring formation, Independence Quadrangle, California.

Streptelasma sp. cf. S. distinctum Wilson
Pl. 109, fig. 6

Description.—Solitary, trochoid; 7 mm. long, 9 mm. by 11 mm. in diameter, cardinal diameter shorter; calyx 4 mm. deep; alternating major and minor septa; 34 major septa, straight to wavy, arranged in quadrants, ends twisted and joined near center at base of calyx; septa of cardinal quadrants bend away from cardinal septum, septa of counter quadrants bend toward counter septum; bending in cardinal quadrants most pronounced nearest cardinal septum, bending in counter quadrants most pronounced nearest alar septa; cardinal septum distinct, not joined with other septa; minor septa very short, 0.25 mm. to 0.50 mm. long in cup and along calyx wall.

Remarks.—This species resembles *S. distinctum* Wilson (1927, p. 12) in number of septa, small size, septal arrangement, and short cardinal diameter, but differs in its straighter and shorter cardinal septum, longer counter septum, and oval cross section. It is probably a distinct species but available material is not adequate for specific description. One specimen was available for study.

Occurrence.—B6095, Johnson Spring formation, Independence Quadrangle, California.

Types.—Hypotype number 37697, deposited in the Museum of Paleontology of the University of California, Berkeley, California.

Streptelasma sp. cf. S. prolongatum Wilson
Pl. 109, fig. 1

Description.—Solitary, trochoid; 35 mm. long, oval, 15 mm. by 25 mm. in diameter, counter quadrants more rounded than cardinal quadrants; 90 alternating major and minor septa, dilate uniformily toward periphery; major septa straight to wavy, ex-

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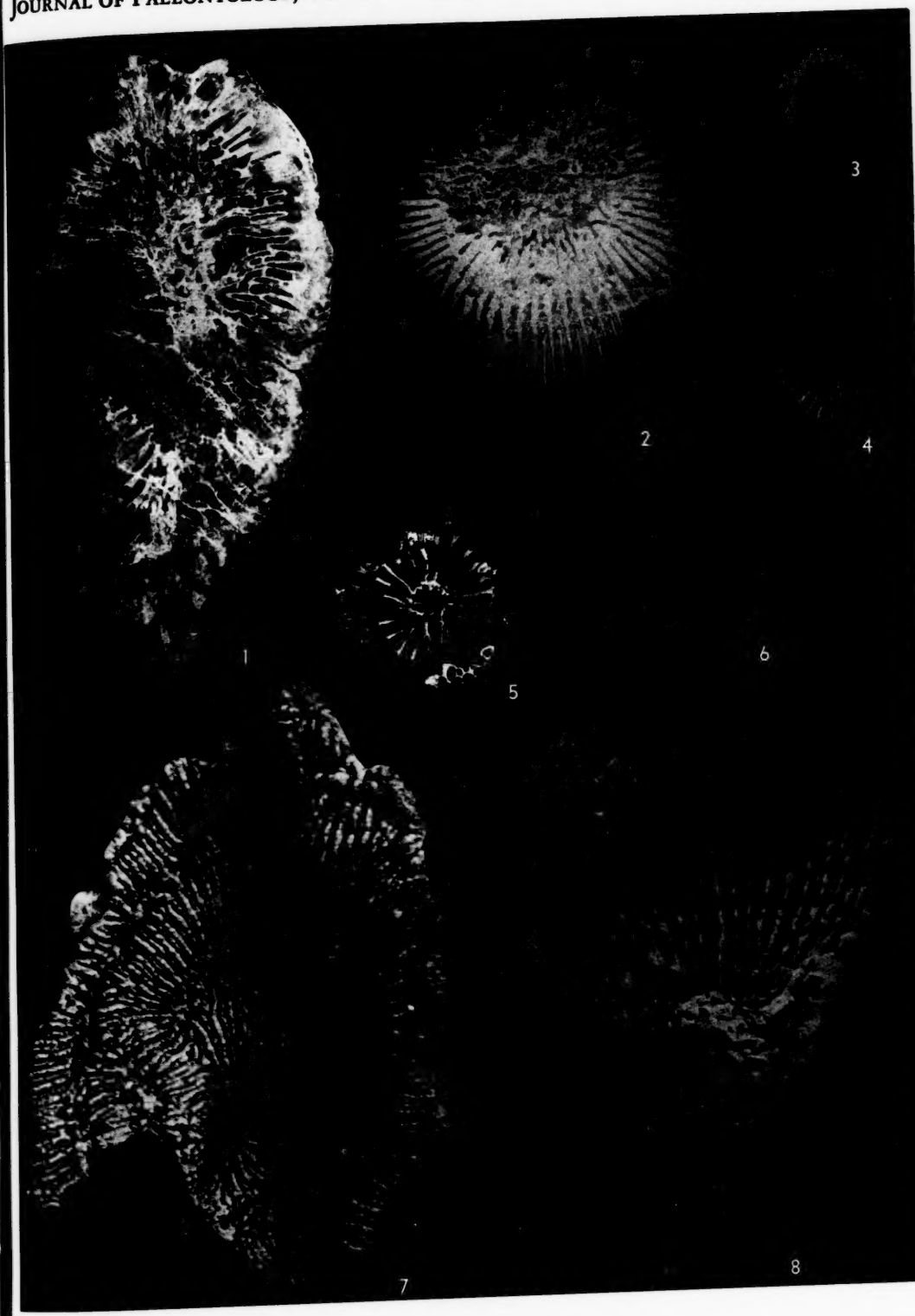
Explanation of Plate 109

Figs. 1.—*Streptelasma* cf. *S. prolongatum* Wilson, transverse section, ×2, hypotype no. 37698.
2—*Streptelasma tennysoni* n. sp., transverse section, ×2, holotype no. 37699.
3,4—*Lambeophyllum* cf. *L. profundum* (Conrad), calicular views of two specimens, ×2; *3* hypotype no. 37695; *4* hypotype no. 37696.
5—*Paleophyllum rugosum* Billings, transverse section, ×2, hypotype no. 37702.
6—*Streptelasma* cf. *S. distinctum* Wilson, calicular view, ×2, hypotype no. 37697.
7—*Anthaspidella inyoensis* n. sp., upper surface, ×2, holotype no. 37694.
8—*Streptelasma tennysoni* n. sp., longitudinal view of fragmentary specimen showing calyx floor and peripheral budding, ×2, paratype no. 37700.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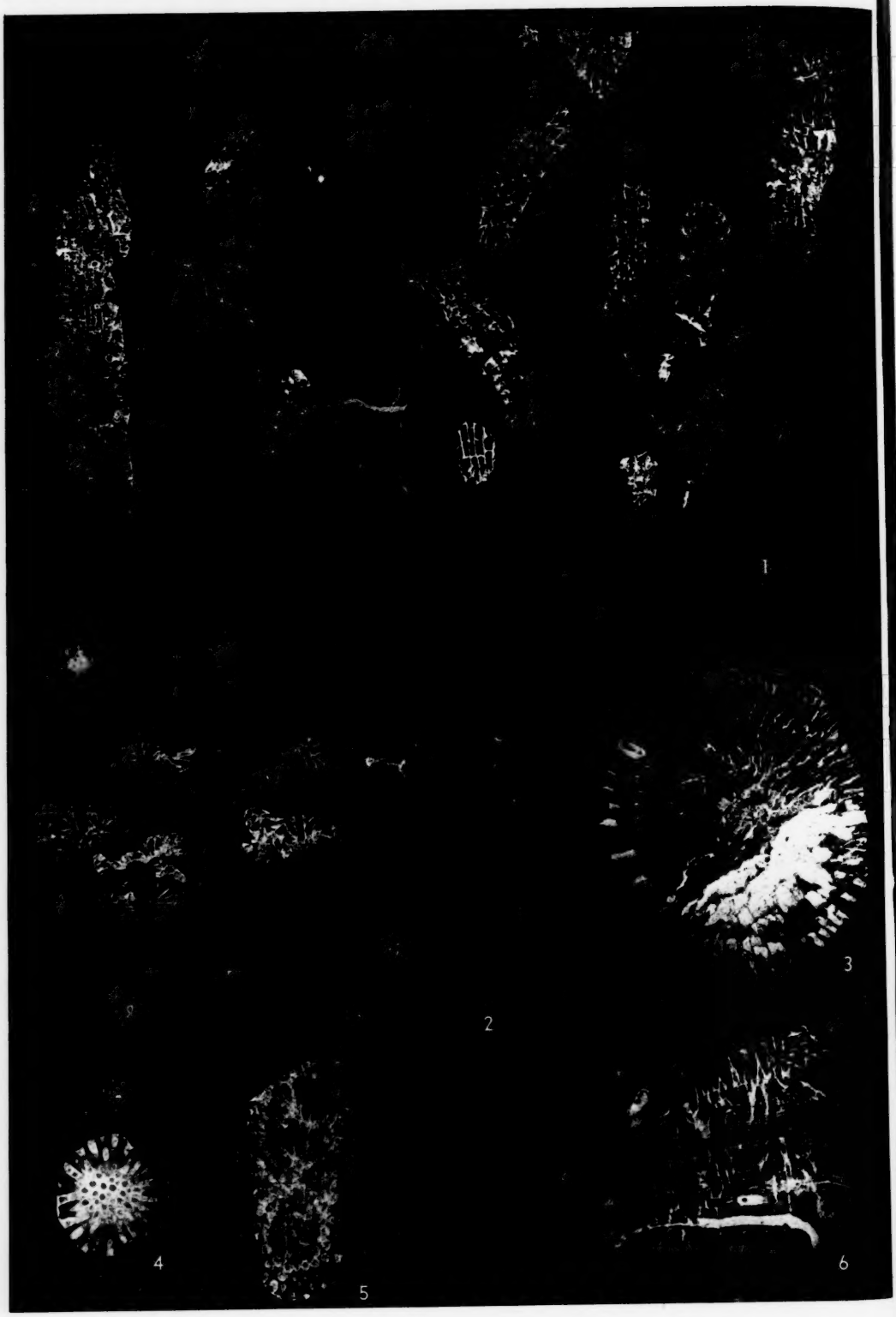
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tending ¾ of the way to the center, 10% with dilate tips; minor septa ½ to ¼ as long as major septa; cardinal septum elongated but imperfectly preserved; septal stereozone ½ mm. to 1 mm. wide; irregular axial structure formed by ends of major septa.

Remarks.—This resembles *S. prolongatum* Wilson (1927, p. 11) in size, shape, number of septa, and elongate cardinal septum, but differs in having well developed minor septa that are not amalgamated in the stereozone. The single available specimen is incomplete and features seen in longitudinal section were not observed.

Occurrence.—B6095, Johnson Spring formation, Independence Quadrangle, California.

Types.—Hypotype number 37698, deposited in the Museum of Paleontology of the University of California, Berkeley, California.

STREPTELASMA TENNYSONI n. sp.
Pl. 109, figs. 2 & 8

Description.—Solitary, trochoid to turbinate; 40 mm. to 60 mm. long (holotype 46 mm. long), oval, 34 mm. in maximum diameter (holotype 24 mm. by 36 mm.); calyx deep, 24 mm. to 40 mm. (holotype 24 mm.), calyx floor upturned; alternating major and minor septa, 76 in holotype, radially arranged; major septa long, straight to wavy, dilated uniformily toward periphery; minor septa up to ½ the length of the major septa, most join major septa; septal stereozone present, 1 mm. to 2.4 mm. wide; tabulae complete, irregular or convex upward, 0.85 mm. to 1 mm. apart; axial structure irregular, formed of twisted septal ends and upturned portions of tabulae; asexual increase by peripheral budding at and near calyx edge.

Remarks.—This species differs from other *Streptelasma spp.* in size, number of septa, and method of budding. It has the upturned calyx floor, septal arrangement, and general dimensions of *S. corniculum* Hall (1847, p. 69), but differs in having more septa and a deeper calyx. This species is gregarious and, though individuals are solitary, they grow adjacent to others and form colony-like masses. This is the most abundant *Streptelasma* in the Johnson Spring formation. Eleven specimens were available for study. The species is named after the English poet.

Occurrence.—B6091, B6093, B6095, B6096, Johnson Spring formation, Independence Quadrangle, California.

Types.—Holotype number 37699, paratype number 37700, deposited in the Museum of Paleontology of the University of California, Berkeley, California.

Genus PALEOPHYLLUM Billings, 1858
PALEOPHYLLUM MAZOURKENSIS n. sp.
Pl. 110, figs. 1,2

Description.—Fasciculate dendroid coralla of varying size; up to 190 mm. long, 100 mm. wide, 110 mm. thick; composed of cylindrical corallites up to 90 mm. long; corallite walls marked by prominent interseptal ridges and fine transverse striations; walls 0.2 mm. to 0.3 mm. thick; corallites circular to oval, from 3.8 mm. to 8.6 mm. and averaging 5.6 mm. in diameter; about 25 major septa in mature individuals; major septa extend ¾ of the distance to the center, straight to wavy, dilated uniformily toward periphery; minor septa absent; stereozone present but narrow; tabulae complete, irregular, concave or convex in parts, edges downturned, 1.7 mm. to 1 mm. and averaging 1.2 mm. apart.

Remarks.—This species somewhat resembles *P. rugosum* Billings (1858, p. 98) and *P. divaricans* Nicholson (1875, p. 216),

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EXPLANATION OF PLATE 110

FIGS. *1,2—Paleophyllum mazourkensis* n. sp., ×2, holotype no. 37701. *1*, longitudinal section; *2*, transverse section. White line indicates edge of thin section.

3,6—Brachyelasma bassleri n. sp., ×2, holotype no. 37705. *3*, transverse section; *6*, longitudinal section.

4,5—Hallopora cf. *H. tolli* Bassler, ×6, hypotype no. 37710. *4*, transverse section, *5*, longitudinal section.

but differs in lacking minor septa. It has tabulae that are wider spaced than those in *P. rugosum*. *P. divaricans* lacks tabulae altogether. *P. mazourkensis* is the most abundant coral in the Johnson Spring formation. Over 20 fragmentary colonies were available for study. The specific name is derived from Mazourka Canyon.

Occurrence.—B6091, Johnson Spring formation, Independence Quadrangle, California.

Types.—Holotype number 37701, Deposited in the Museum of Paleontology of the University of California, Berkeley, California.

PALEOPHYLLUM RUGOSUM Billings
Pl. 109, fig. 5

Paleophyllum rugosum Billings, E., 1858, p. 168.
Columnaria rugosa (Billings), Lambe, L. M., 1899, p. 297.
Favistella aff. F. discreta, Langenheim, *et al.*, 1956, p. 2093.

Description.—Cylindrical corallites, 14 mm. to 24 mm. long, diameter 6 mm. to 8 mm.; 24 major septa extend $\frac{3}{4}$ to $\frac{4}{5}$ of the distance to the center, straight to wavy, dilated uniformily toward periphery; stereozone present, $\frac{1}{2}$ mm. wide; minor septa present between some of the major septa (at least 12 present), short, $\frac{1}{4}$ the length of the major septa to mere bumps on the inner side of the stereozone; tabulae thin, closely spaced, about 0.5 mm. apart, complete, edges downturned, centers flat or sagging.

Remarks.—Polished longitudinal and one transverse thin section were made of material identified as *Favistella aff. F. discreta* by Langenheim *et al.* (1956, p. 2093). The features exhibited by these sections are those of *Paleophyllum rugosum*. Three separate and fragmentary corallites were available for study.

Occurrence.—B963, Johnson Spring formation, Independence Quadrangle, California.

Types.—Hypotype number 37702, deposited in the Museum of Paleontology of the University of California, Berkeley, California.

Genus GREWINGKIA Dybowski, 1873
GREWINGKIA WHITEI n. sp.
Pl. 111, figs. 1,2,6

Description.—Solitary, fragmentary; 41 mm. to 73 mm. long, oval to circular in cross section, 35 mm. to 40 mm. in maximum diameter, trochoid to ceratoid (some specimens laterally compressed); 99 to 107 alternating major and minor septa; major septa wavy to zig-zag, short, extend $\frac{1}{3}$ to $\frac{1}{2}$ the distance to the center, thin but dilate near periphery; minor septa $\frac{1}{2}$ to $\frac{2}{3}$ the length of the major septa; $\frac{1}{3}$ to $\frac{1}{2}$ septa with lobed ends; wide loose axial structure present, formed of upturned tabulae and septal plates; septal stereozone present, $\frac{1}{2}$ mm. to 1 mm. wide; tabulae complete, irregularly flat to convex upward, edges downturned, 0.9 mm. to 1 mm. apart.

Remarks.—Shorter septa and a wider axial structure differentiate this species from European ones. It has fewer septa and flatter tabulae than the type species, *G. kiaeri* Wedekind (Scheffen, 1933, p. 21). *G. rusticum* (Billings) (1858, p. 98) resembles *G. whitei* but has fewer septa. Two nearly complete specimens were available for study. This species is named after T. H. White, English author and medieval scholar.

Occurrence.—B6091, Johnson Spring formation, Independence Quadrangle, California.

Types.—Holotype number 37703 and paratype number 37704 deposited in the Museum of Paleontology of the University of California, Berkeley, California.

Genus BRACHYELASMA Lang, Smith, & Thomas, 1940
BRACHYELASMA BASSLERI n. sp.
Pl. 110, figs. 3,6; pl. 3, fig. 3

Streptelasma sp., Langenheim, *et al.*, 1956, p. 2093, in part.

Description.—Solitary, ceratoid to trochoid near base, cylindrical in upper portion; 55 mm. to 85 mm. long (holotype 85 mm.), minimum diameter 18 mm. to 32 mm. (holotype 32 mm.); alternating major and minor septa, straight to wavy becoming zig-zag in part, dilated uniformily toward periphery; major septa extend $\frac{1}{4}$ to $\frac{1}{2}$ the distance to the center; minor septa $\frac{1}{3}$ to $\frac{1}{2}$ as long as major septa; 5% or fewer septa with dilated axial ends; septa radially arranged, 105 in a section of the holotype 25 mm. in diameter, 50 in a section of the holotype 10 mm. in diameter, 108 to 83 in sections of 30 mm. to 18 mm. by 28 mm. in diameter; septal stereozone narrow, 0.25 mm. to 1.0 mm. thick

wall thin, ½ mm. to 1 mm. thick; tabulae complete, edges downturned, central portion flat to sagging, horizontal to sloping, irregularly but closely spaced, averaging 0.45 mm. apart in the holotype, 0.8 mm. to 1.4 mm. apart in other more poorly preserved specimens; axial structure absent.

Remarks.—This species differs from European species in having a larger number of septa, closer spaced tabulae, and zig-zag septa. These corals were placed in the genus *Brachyelasma* because they have short septa, lack an axial structure, and have only a few axial septal lobes. This is the first noted occurrence of *Brachyelasma* in N. America, but it seems probable that many specimens now identified as *Streptelasma* actually will be found to be *Brachyelasma spp.* Four well preserved specimens were available for study. This species is named after R. S. Bassler.

Occurrence.—B963 and B6091, Johnson Spring formation Independence Quadrangle, California.

Types.—Holotype number 37705 and paratype number 37706 deposited in the Museum of Paleontology of the University of California, Berkeley, California.

Order TABULATA Milne-Edwards & Haime, 1850
Family CHAETETIDAE Milne-Edwards & Haime, 1850
Subfamily LICHENARIINAE Okulitch, 1936
Genus LICHENARIA Winchell & Schuchert, 1895

LICHENARIA (?) sp. cf. L. HEROENSIS (Raymond)
Pl. 112, figs. 9,10

Description.—Corallum hemispherical, ceroid, 35 mm. long, 25 mm. wide, 25 mm. high; corallites polygonal, 3 to 7 sided, generally 5 or 6 sided, 1 mm. to 1.6 mm. in diameter; walls 0.1 mm. thick, amalgamated; septa absent, a few corallites show irregularly spaced bumps that may represent septal ridges; tabulae complete, generally flat to convex upward, a few sagging or flat with up-pointed centers, ⅛ to ⅓ as thick as walls, zones of close and far spacing present but grading into one-another, 1 mm. to 1.2 mm. apart in widely spaced zone, 0.7 mm. to 0.8 mm. apart in closely spaced zone.

Remarks.—This specimen resembles those described by Bassler (1950, p. 260.) as *L. heroensis* (Raymond) and those described by Okulitch (1936, p. 63) as *Lamontia heroensis* Raymond in all respects but one. The tabulae are generally flat or bend upward in the specimen from the Johnson Spring formation and not downward as in the specimen examined by Bassler and Okulitch. Okulitch (1936, p. 63) described mural pores in *L. heroensis* and placed it in the genus *Lamontia.* Bassler (1950, p. 260.) states that these pores are crystals of calcite penetrating the walls and places the species in the genus *Lichenaria.* My specimen resembles the descriptions of the species *heroensis*, but whether this species belongs in the genus *Lamontia* or in the genus *Lichenaria* is uncertain. I questionably place this new specimen in the genus *Lichenaria* because it does not have mural pores. One fragment of a larger colony was available for study.

Occurrence.—B6091, Johnson Spring formation, Independence Quadrangle, California.

Types.—Hypotype number 37707 deposited in the Museum of Paleontology of the University of California, Berkeley, California.

LICHENARIA SISYPHI n. sp.
Pl. 111, fig. 4

Lichenaria carterensis (Safford), Langenheim, *et al.*, 1956, p. 2093.

Description.—Corallum hemispherical, ceroid, 45 mm. long, 39 mm. wide, 39 mm. high; corallites polygonal, 4 to 7 sided, generally 6 sided, 1.4 mm. to 1.9 mm. in diameter, averaging 1.6 mm. in diameter; walls amalgamated, 0.09 mm. to 0.14 mm. thick; septa absent in most corallites, 0.2 mm. or shorter ridges, up to 9 in number, present in a few corallites, ridges irregularly arranged; tabulae complete, edges downturned, generally convex upward, a few flat, wavy, or sagging, ½ to ⅓ as thick as the walls, spaced about 1.1 mm. apart.

Remarks.—This species resembles species of the genus *Nyctopora* in having some septal development, but there are no distinguishable double walls between the corallites. In corallite diameter it is closest to *L. carterensis* (Safford) (1896, p. 285), *L. typa* Winchell and Schuchert (1895, p. 83.) and L. *coboconkensis* Okulitch (1939, p. 514). It differs from *L. typa* and *L. carterensis* in

having closer spaced tabulae and convex tabulae. It differs from *L. coboconkensis* in having closer spaced and more irregular tabulae. It differs from all three in not having alternating zones of closely and widely spaced tabulae.

This coral was previously identified as *L. carterensis* (Langenheim, *et al.*, 1956, p. 2093.) without the aid of thin sections. All features described above were observed in longitudinal and transverse thin sections. One fragmentary corallum was available for study. The species is named after Sisyphus mythical king of Corinth.

Occurrence.—B963, Johnson Spring formation, Independence Quadrangle, California.

Types.—Holotype number 37708 deposited in the Museum of Paleontology of the University of California, Berkeley, California.

Family AULOPORIDAE Milne-Edwards & Haime, 1850
Subfamily SYRINGOPORINAE Nicholson, 1879
Genus EOFLETCHERIA Bassler, 1950
EOFLETCHERIA KEARSARGENSIS n. sp.
Pl. 111, fig. 5; pl. 112, fig. 1

Description.—Fasiculate, phaceloid corallum, 44 mm. long, 19 mm. wide, 24 mm. high; corallites circular to oval, tubular, 1.1 mm. to 1.7 mm. in diameter, averaging 1.4 mm. in diameter; 14 to 20 corallites per square centimeter, averaging 17 per square centimeter, interspaces up to 3 times the corallite diameter; walls solid, 0.2 mm. to 0.4 mm. thick; septa absent; tabulae complete and incomplete, about 0.8 mm. apart in the uncrowded zone, about 0.3 mm. apart in the crowded zone.

Remarks.—*E. kearsargensis* differs from the three other species of *Eofletcheria* found in North America. It has more closely spaced tabulae and wider interspaces than *E. laxa* Bassler (1950, p. 266), and wider corallites and more closely spaced tabulae then *E. incerta* (Billings) (in Bassler, 1950, p. 266). *E. sinclairi* Okulitch (1937, p. 315) is non tabulate and has narrower corallites. One well preserved but fragmentary colony was available for study. The species is named after the Kearsarge Railroad station in the Independence Quadrangle.

Occurrence.—B6094, Johnson Spring formation, Independence Quadrangle, California.

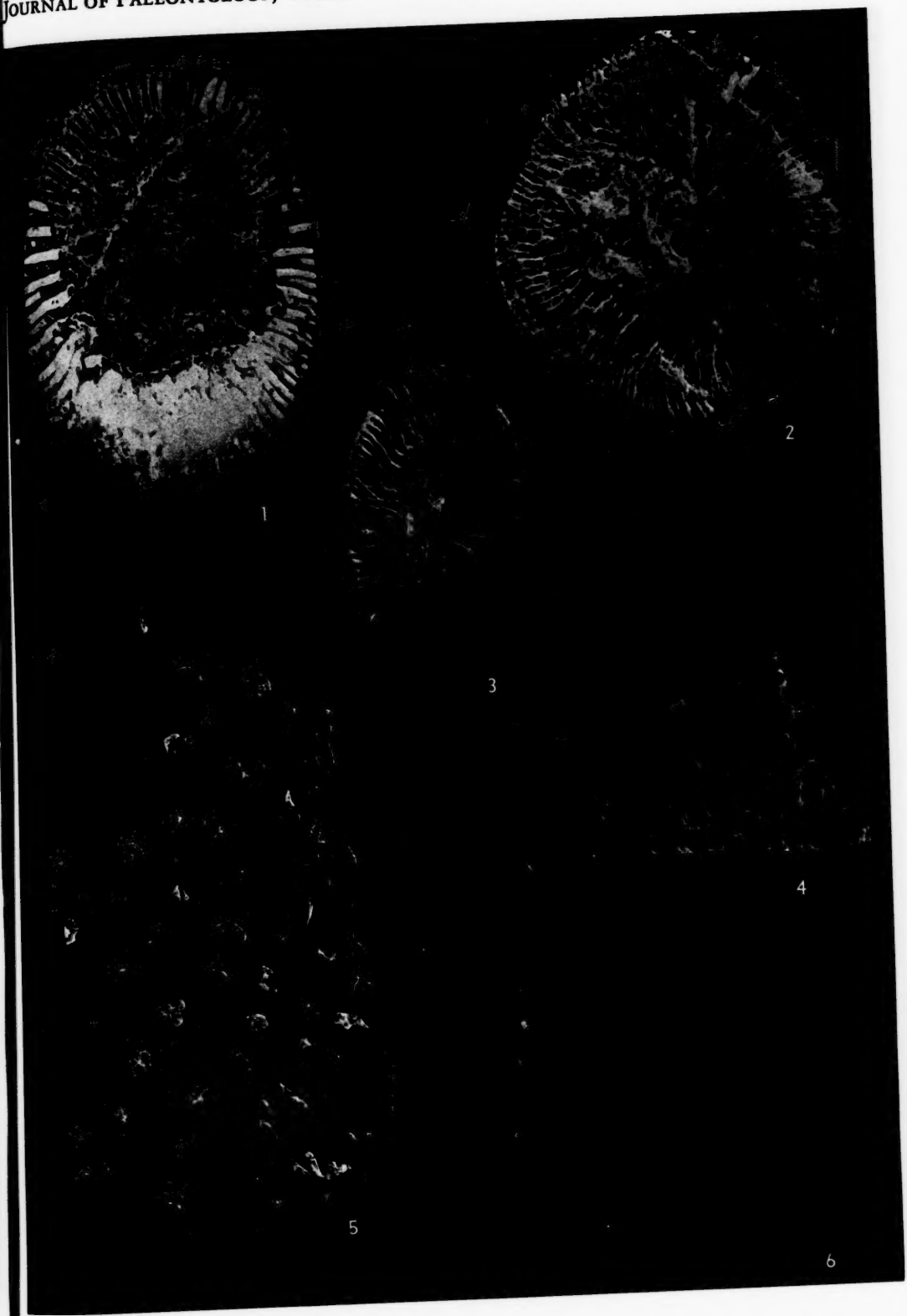
Types.—Holotype number 37709 deposited in the Museum of Paleontology of the University of California, Berkeley, California.

Phylum BRYOZOA Ehrenberg, 1831
Class ECTOPROCTA Nitsche, 1869
Subclass STENOLEMATA Borg, 1926
Order TREPOSTOMATA Ulrich, 1882
Suborder INTEGRATA Ulrich & Bassler, 1904
Family HALLOPORIDAE Bassler, 1911
Genus HALLOPORA Bassler, 1911
HALLOPORA sp. cf. H. TOLLI Bassler
Pl. 110, figs. 4,5

Description.—Ramose cylindrical zoarium, 8 mm. long, diameter 4 mm.; zooecia erect axially, bent outward peripherally, 0.2 mm. to 0.4 mm. in diameter, averaging

EXPLANATION OF PLATE 111

FIGS. *1—Grewingkia whitei* n. sp., ×2, transverse section, paratype no. 37704.
2—Grewingkia whitei n. sp., ×2, transverse section, holotype no. 37703.
3—Brachyelasma bassleri n. sp., ×2, transverse section, paratype no. 37706.
4—Lichenaria sisyphi n. sp., ×2, transverse section, holotype no. 37708.
5—Eofletcheria kearsargensis n. sp., ×4, transverse section, holotype no. 37709.
6—Grewingkia whitei n. sp., ×2, longitudinal section, holotype no. 37703.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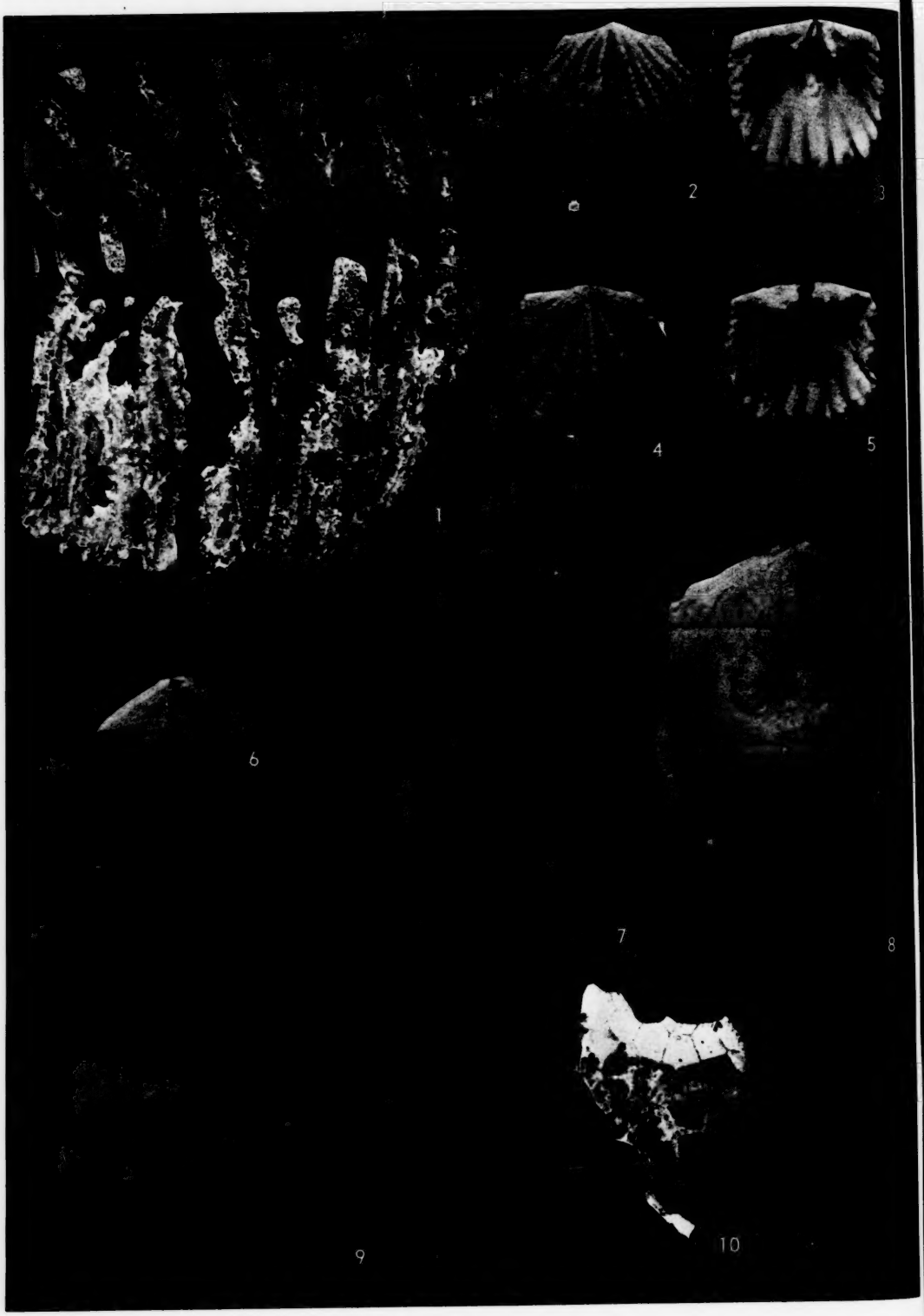
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0.3 mm. in diameter, polygonal, 5 or 6 sided, angles often rounded producing oval or circular outline; adjacent walls separated by a faint dark line; acanthopores absent; mesopores present, $\frac{1}{4}$ to $\frac{1}{2}$ the size of the normal zooecia; zooecial diaphragms 0.2 mm. to 0.6 mm. apart, spaced closer in the mature region, flat, generally inclined; mesopore diaphragms closely spaced, about 15 per mm.

Remarks.—This specimen resembles *H. tolli* Bassler (1911, p. 233) in zoaria shape, abundance of mesopores, and spacing of diaphragms; however it has a smaller zoarium and smaller more rounded zooecia. The single available specimen is not sufficient to describe a new species.

Occurrence.—B6091, Johnson Spring formation, Independence Quadrangle, California.

Types.—Hypotype number 37710 deposited in the Museum of Paleontology of the University of California, Berkeley, California.

Phylum BRACHIOPODA Dumeril, 1806
Class INARTICULATA Huxley, 1869
Order ATREMATA Beecher, 1891
Superfamily LINGULACEAE Waagen, 1885
Family LINGULIDAE Gray, 1840
Genus LINGULASMA Ulrich, 1889
LINGULASMA (?) sp.
Pl. 112, figs. 7,8

Description.—16 mm. to 34 mm. long, 11 mm. to 28 mm. wide, widest anteriorly; biconvex; commisure rectimarginate, anterior margin truncate, lateral margin gently curved, posterior margin more sharply curved to form apical angle of 99 degrees; two low diverging ridges extending from near the apex to at least $\frac{1}{3}$ the length of the ventral valve; stronger median ridge extends from apex to at least $\frac{1}{2}$ the length of the dorsal valve; muscle scars not preserved; shell finely punctate.

Remarks.—The specimens are poorly preserved and only one was sectioned. This specimen showed the prominent median ridge characteristic of the dorsal valve of *Lingulasma*. The anterior edge of the ventral valve exhibits the remnants of papillate ornamentation. But the absence or nonpreservation of platforms in either valve makes the identification uncertain. Six specimens were available for study.

Occurrence.—B6091, Johnson Spring formation, Independence Quadrangle, California.

Types.—Hypotype number 37711 deposited in the Museum of Paleontology of the University of California, Berkeley, California.

Class ARTICULATA Huxley, 1869
Suborder ORTHOIDEA Schuchert & Cooper, 1931
Superfamily ORTHACEA Walcott & Schuchert, 1908
Family ORTHIDAE Woodward, 1852
Subfamily GLYPTORTHINAE Schuchert & Cooper, 1931
Genus PTYCHOPLEURELLA Schuchert & Cooper, 1931
PTYCHOPLEURELLA ARTHURI n. sp.
Pl. 112, figs. 2–6

Ptychopleurella n. sp., Langenheim, *et al.*, 1956, p. 2093.

EXPLANATION OF PLATE 112

FIGS. *1*—*Eofletcheria kearsargensis* n. sp., ×4, longitudinal section, holotype no. 37709.
2–6—*Ptychopleurella arthuri* n. sp., ×5. *2*, dorsal exterior, paratype no. 37713; *3*, dorsal interior, holotype no. 37712; *4*, ventral exterior, paratype no. 37714; *5*, ventral interior, paratype no. 37715; *6*, ventral posterior, paratype no. 37716.
7,8—*Lingulasma* (?) sp., ×2, hypotype no. 37711. *7*, ventral valve; *8*, dorsal valve. Lines show area removed in sectioning.
9,10—*Lichenaria* (?) cf. *L. heroensis* (Raymond), hypotype no. 37707. *9*, ×2, longitudinal section, *10*, ×4, transverse section.

Description.—Impunctate; outline megathyrid; anterior margin sulcate; multicostate; costae sharp, high, lamellose, 11 to 16 costae on immature valves, 33 on mature valve; ventral valve has high median costae; dorsal valve has sulcus bounded by two prominent costae, sulcus contains two smaller costae; ventral valve subpyramidal; interarea procline, high, horizontally striated; delthyrium slitlike, constricted by lateral plates; teeth supported by short lamellae; dorsal valve convex, deeply sulcate; interarea orthocline, short, curved; notothyrium triangular, well developed notothyrial platform present; dental sockets between brachiophore and inner wall; brachiophore short, rod-like, of *Orthis-Hesperorthis* type (Schuchert & Cooper, 1932, p. 37); cardinal process weak, thin, platelike; prominent median ridge bisects interior of dorsal valve, extends anteriorly from base of notothyrial platform.

Holotype and Paratype Measurements

Mature Ventral Valve—length 9 mm., width 13 mm.
Immature Ventral Valves—length 4 mm. and 4.5 mm., width 5.5 mm. and 6 mm.
Immature Dorsal Valves—length 5 mm., 5 mm., and 4.3 mm., width 5.5 mm., 5.5 mm., and 5 mm.

Remarks.—This species differs from other North American species in its large size and numerous costae. It is closest in size to *P. lamellosa* (Twenhofel) (1914, p. 24) but has more numerous costae. Other North American species are much smaller and have fewer costae than the immature forms of *P. arthuri.* One mature ventral valve and over thirty immature dorsal and ventral valves were available for study. This species is named after the legendary ruler of ancient Britain.

Occurrence.—B963 and B6096, Johnson Spring formation, Independence Quadrangle, California.

Types.—Holotype number 37712 and paratypes numbers 37713, 37714, 37715, 37716, 37717, deposited in the Museum of Paleontology of the University of California, Berkeley, California.

LOCALITY DESCRIPTIONS

All localities are referred to the U. S. Geological Survey Independence Quadrangle, Califiornia, 15 minute series. All samples were collected by this author unless stated otherwise.

B962—Dolomite 140 feet above the base of the Johnson Spring formation in the First South Section.
B963—Limestone 90 feet above the base of the Johnson Spring formation in the First South Section.
B966—Limestone 50 feet above the base of the Johnson Spring formation in the First South Section.
B989—Limestone 162 feet above the base of the Johnson Spring formation in the Lead Canyon Trail Section.
B990—Limestone 145 feet above the base of the Johnson Spring formation in the Lead Canyon Trail Section.
B991—Interbedded limestone, quartzite, quartzitic siltstone, and shale 135 feet above the base of the Johnson Spring formation in the Lead Canyon Trail Section.
B992—Limestone 71 feet above the base of the Johnson Spring formation in the Lead Canyon Trail Section.

All of the above localities were collected by Langenheim, *et al.* (1956).

B6091—Nodular to massive limestone below the uppermost quartzite of the Johnson Spring formation on the north side of Lead Canyon.
B6092—Float same locality as B6091.
B6093—Limestone float below interbedded limestone and quartzite unit that is below the upper two quartzites of the Johnson Spring formation on the south side of the large spur south of the two faults that are south of Barrel Springs.
B6094—Dolomite float above the basal quartzite of the Johnson Spring formation on the north side of the first canyon south of Lead Canyon.
B6095—Limestone below the fourth quartzite from the base of the Johnson Spring formation on the north side of the first canyon south of Lead Canyon.
B6096—Limestone above the quartzite that overlies B6095.
B6097—Limestone float between the upper two quartzites of the Johnson Spring formation on the north side of the first canyon south of Lead Canyon.

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STUDIES OF THE WESTERN CANADA STRINGOCEPHALINAE*

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ABSTRACT—Three new and one old species of *Stringocephalus* are described and credited to occurrence positions in the Middle Devonian of Western Canada. The types of all four species are from the northern Rocky Mountains. Other occurrences are listed from Lake Winnipegosis outcrops, several boreholes across Saskatchewan and Alberta, and other outcrops in northern Alberta, northeastern British Columbia, and the Northwest Territories. Formation nomenclature is examined and paleogeography is interpreted.

INTRODUCTION

STRINGOCEPHALINAE, including the well-known type genus and the much less known *Geranocephalus*, are the most distinctive and peculiar faunal element in the Western Canada Middle Devonian. Geographically, *Stringocephalus* ranges from the south of England, through north-western and northern Europe, northern and eastern Asia, into north-western America, and to the south-east as far as Manitoba. This series of occurrences epitomizes not only the collective range of the tribe but the probabilities of its close continuity and connection with both a circumboreal origin and an exclusively separate existence from the better known New York-Michigan Middle Devonian region which is Atlantic with perhaps tropical connections.

Minor attempts have been made to employ the forms of *Stringocephalus* (always collectively, however, never analytically) as evidence not only of correlation and paleogeography but also of ecologic conditions. It has seemed hopeful that the combination of paleogeographic and ecologic deductions might permit here and there reconstruction of sedimentary environments. So far, it is too much to say that there has been any success; in fact, the more that is discovered, the more refractory and even contradictory the evidence appears. At some places, *Stringocephalus* is collected in pale biohermal dolomites, at others, in black shales. Could one envisage a much greater ecological discrepancy?

In the meantime, geological exploration, particularly that which is pursued with the objective of discovering petroleum, runs more and more into regions of northern North America where Middle Devonian is either a key formation or the economically prospective deposit. That being so, it is desirable to neglect no studies the outcome of which might be of aid in the path of exploration. It has seemed to the writer for some time that better understanding of the Stringocephalinae could serve this end. Hitherto, neither collections nor stratigraphic occurrence data have been sufficiently good to permit of much analysis, and progress has been confined to minor stratigraphic work and to half-hearted protests against attaching the European species name *burtini* indiscriminately to every Stringocephaline brought in. However, more detailed field-work and better collecting have been done lately, and it is now possible to make another small but positive step forward. This will consist in making known certain very distinct forms of *Stringocephalus* distributed in three separable zones, and in an attempt to solve the contradictory aspects of the ecology problem.

OCCURRENCES

The *Stringocephalus* forms in the Winnipegosis formation were recorded as one species by Whiteaves (1890)* who listed as

* The writer acknowledges permission to publish granted by Imperial Oil Limited, Husky Oil & Refining, Phillips Petroleum Company, Sohio Petroleum Company, and Bear Oil Company.

* This was the first record of *Stringocephalus* in North America. With it one usually couples Whiteaves' (1892) full paleontological report. The

S. burtini some of the species described herein. His large transverse form from the west side of Lake Winnipegosis appears to be *S. chasmognathus* which is the common Winnipegosis species; some of the smaller ones are the young of that species, others may be *glaphyrus, sapiens* or even *Geranocephalus*. These occur in a very light colored, cream to buff, granular, fragmental to reefal limestone—becoming here and there dolomite. The accompanying fauna includes the distinctive *Atrypa perfimbriata, Spinatrypa andersonensis*, large and very thick shelled pelecypods and gastropods many of which have perfectly preserved external ornament, large crinoid columnals still in long articulated series, large ostracods similar to *Isochilina*, a sponge *Sphaerospongia tessellata*, and a profusion of very large rugose as well as tabulate corals, and numerous large bulbous stromatoporoids. Notably, *Caunopora* is lacking. In general, the specimens are not wave-worn in the least, though a few are broken as if cracked by a fall or a clean blow before deposition in the original sediment.

In Sohio Marysburg No. 1 (16-29-38-22W2)* *Stringocephalus* cf. *sapiens* occurs with *Spinatrypa* cf. *andersonensis*, some solitary rugose corals, the tabulate coral *Thamnopora* and many reef-making stromatoporoids at 2663 feet in a light buff-grey, coarse-grained, granular limestone. The occurrence demonstrates that the interval 2650 to 2743 feet is the Winnipegosis formation, and that the red, silty shale 2620 to 2650 is the First Red or Mafeking formation which here includes the much diminished equivalent of the First Salt of the Elk Point formation. *Atrypa perfimbriata* appears at 2691 feet. It is recognized that these interpretations are at variance with those of Baillie (1953).

In Husky-Phillips Fitzmaurice No. 1 (16-18-27-8W2) *S. chasmognathus* occurs at 3105–32 feet with a coral and stromatoporoid fauna similar to that of Marysburg and in a buff-colored, fine-grained, granular limestone. The interval 3095 to 3240 is the Winnipegosis; that from 3015 to 3065 is the First Red or Mafeking; the First Salt of the Elk Point here begins to be distinctive—it is the gypsum and salt formation, 3065 to 3095 feet.

In Sohio Findlater No. 2 (9-20-20-25W2), *S. chasmognathus* appears at 4742–52 feet with *Atrypa perfimbriata* and the same fauna of corals and corallines. As with other Saskatchewan and Manitoba stations, the chief lack is *Caunopora* and cystiphylloids. The rock is identical with the Fitzmaurice occurrence. The interval 4630 to 4830 is the Winnipegosis, and, since the evaporite interval 4421 to 4630 is the Davidson Salt, that evaporite is the equivalent of First Salt. The true equivalent of Elk Point top comes at 4330 feet.

In all these occurrences, the coarse grain, the fragmental to reefal character of the rock, the notable thickness of the skeletal parts of many of the fossils, all lead to the conclusion that the beds with *Stringocephalus* were deposited in shallow water. This conclusion seems to be equally true of such an area as Lake Winnipegosis which can only have lain near the east edge of the Middle Devonian basin, and such an area as Findlater which lay well into the midst of it. It may be well to note again that these remarks make sense only if one has abandoned the correlations advocated by Baillie (1953) between outcrop formations in Manitoba and their supposed sub-surface equivalents.

This type of occurrence is repeated in Bear Rodeo No. 1 (Lot 5, McMurray Settlement, Tp. 89, R. 9W4) in which, from 890 to 920 feet, *S. chasmognathus* occurs in a fragmental limestone, with coarse to fine, granular matrix, of pale buff to dark brown color, and containing also whole and much broken pieces of *Atrypa perfimbriata, Spina-*

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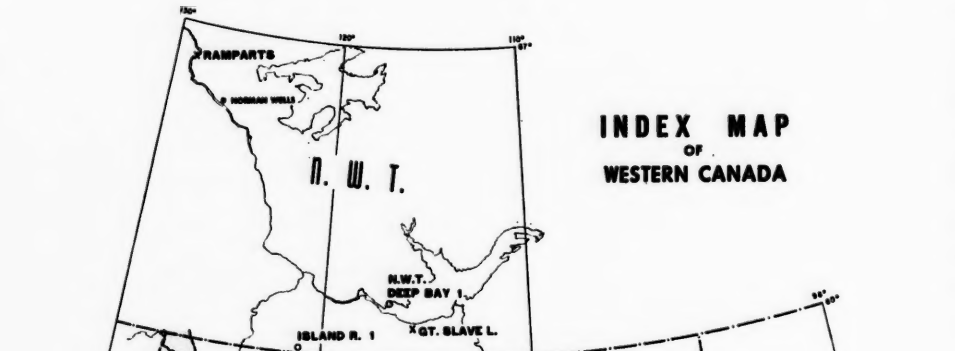
second record was Whiteaves' (1891) notice of McConnell's collection from the Ramparts of the MacKenzie. Earlier, Meek (1867, p. 66–67) had noted the "Terebratulae" of Great Slave Lake which we now recognize as stringocephalines. Meek quoted also Woodward (whose work has been seen neither by the writer nor by the compilers of the valued "Bibliography of North American Geology," though, plainly, Meek had seen it) and refers to collections in the Canadian north by Sir John Franklin and Sir John Richardson.

* This is the geographical location in accordance with the western Canadian plan of land designation: it means Legal Subdivision 16, of Section 29, in Township 38, Range 22 west of the 2nd Meridian.



TEXT-FIG. *1*—Index map of western Canada.

trypa andersonensis, *Ambothyris sublineata*, *Thamnopora* sp., cystiphylloid solitary corals and numerous stromatoporoids though mainly, in fact almost entirely, of bulbous types. The Rodeo 1 section is important in that from 940 to 960 feet the much older *Atrypa arctica* fauna has been recovered. Plainly, then, this lower part of the carbonate sequence is the correlative not of Winnipegosis and Presqu'ile formations but of Elm Point and Pine Point.

This discovery has some consequences for stratigraphic nomenclature and the meaning of some stratigraphic terms. Not far from Rodeo 1 is the type section of Methy formation in Bear Westmount No. 2 between depths 562 and 775 feet (Greiner, 1956). From lithological comparison it is evident that this section is directly correlative with that in Rodeo 1 from 848 to 960 feet. The inevitable conclusion is that Methy formation is equivalent to Winnipegosis, second Elk Point salt and Elm Point formation.

With regard to the outlines of this Middle Devonian basin, the last occurrence might be said to be marginal. Much closer to the center of the basin, yet different only in minor degree, is an occurrence of *Stringocephalus* sp. ind. in Imp. Darling No. 1 (16-19-62-19W4) at 5100 feet, associated with *Spinatrypa andersonensis*, *Spongophyllum pax*, cystiphylloid corals, and *Caunopora* sp.—the first of *Caunopora*, as one goes

north, is noteworthy here. The rock is a buff to brown, fine grained, granular limestone with numerous scattered fossils—the occurrence being 180 feet below the top of the limestone member (that is, member 3 or Winnipegosis correlative) in which it occurs, and 510 feet below the top of the Elk Point formation. The deposit is remarkably similar to the basin margin rocks; it is distinctive chiefly in that among the stromatoporoids only ramose types are present; furthermore the deposit is fine grained, is fragmental only in certain thin beds, is not reefal, and, considered as a whole and including strata in which neither *Stringocephalus* nor the corallines occur, it is slightly argillaceous.

The occurrence of S. *chasmognathus* in Imp. Surette Lake No. 1 (15-24-109-17W5) at 3857–3881 is similar to the last. The rock is a buff-colored, fine grained, granular limestone with numerous scattered fossils, many of them broken in pieces. They include mostly *Caunopora* sp., *Thamnopora* sp., and other corallines.

Similar to such basin-margin occurrences as Bear Rodeo 1 are the outcrops on the south shore of Great Slave Lake (in which *Stringocephalus* was discovered by Kindle, 1921) where the Presqu'ile formation bears, in a zone of light colored, fragmental to reefal, magnesian limestone, *S. chasmognathus* and *S. sapiens*. These beds come about 200 to 300 feet below the limestone top, and several hundred above the base of Middle Devonian which lies on Pre-Cambrian on Slave River, there being Middle Devonian fossils, e.g. *Spongophyllum* sp., down to within 6 feet of the Archaean basement. Some maps, issued as recently as 1950, still showed a Silurian formation on Slave River; however, in the writer's observation this formation was merely a mistakenly correlated basal part of the Devonian. Somewhat similar stratigraphic relationships exist in N.W.T. Deep Bay No. 1, on the north-west shore of Great Slave Lake, in which at 655 feet below surface, *Stringocephalus* sp. ind. occurs in a reefal limestone with corals and stromatoporids including *Caunopora* as well as bulbous types, 265 feet below the top of the formation (that is, below the base of Horn River black shale). Here, as elsewhere in the Devonian of western Canada, the main body of reef is composed of stromatoporoids.

In the vicinity of Norman Wells, N.W.T., where the Middle Devonian oil-producing reef, or Ramparts formation, is, in the main, coarse grained, granular limestone, thickly studded with (in places almost entirely composed of) stromatoporoids of all various growth types, *S. sapiens* occurs in certain dense, fragmental limestone layers. With it are other brachiopods and mollusks. Its position is about 400 feet below the top of the formation, that is, below the base of the Fort Creek shale. Specifically, it was recovered from the Morrow Creek well at 1090 feet depth. *S. chasmognathus* and an undetermined species related to *S. sapiens* occur at the Ramparts of the MacKenzie, the type outcrop, at 180 to 220 feet below the exposed limestone top.* This occurrence is 100 miles downstream from Norman Wells. It is notable for the occurrence of a species of *Renssellandia* in the basal Ramparts limestone—supposedly a link with the American Middle west and even with Pennsylvania (by a roundabout route).

In the mountains 120 miles south-west of Norman Wells, *Stringocephalus* reappears in formations of the same age but of entirely different lithic character. The rock is a very dark grey, argillaceous limestone; it bears *Stringocephalus* sp. ind. and *Favosites* sp. It is evident in this lithic character that an entirely different paleogeographic province is represented; this we shall now explore.

Turning again southward, to a point only just within the Northwest Territories and located in the plains 100 miles east of the

* Geological investigation of Norman Wells area has led to the strange result that in the oilfield vicinity Ramparts formation goes by the name of Kee Scarp, whereas the name Ramparts is there applied to the basal Devonian limestone with which true Ramparts formation has no connection. Some day, no doubt, this will be corrected. The basal Devonian limestone at Norman Wells is the Norman Wells formation. In Discovery No. 3, from depth of 2010 feet to 2570 feet we have a type section consisting of 110 feet of limestone, 250 of somewhat argillaceous strata, and 200 feet of limestone, in descending order. The typical fossils are *Billingsastraea arachne* and *Schuchertella* n. sp. The formation is overlain by Hare Indian shale; it is underlain by Bear Rock dolomite.

mountain front, Imperial Island River No. 1, N. lat. 60°9′18″, W. long. 121°8′16″, exhibits a Middle Devonian deposit similar to the last. *S.* cf. *sapiens*, *Atrypa perfimbriata*, *Spinatrypa* sp., *Ambothyris* cf. *sublineata*, *Schizophoria* sp., unrecognizable *Crinoids*, *Thamnopora* sp., and stromatoporoids occur at 7370 feet depth in a very dark grey, argillaceous limestone with black shale interbeds. The fossils are mostly whole, some are articulated; but in some beds some of them are in pieces; the crinoids throughout the formation are in isolated columnals. The occurrence is 450 feet below the top of the limestone formation or base of the Fort Creek shale equivalent.

Still farther south, and within the mountains, Redfern Lake, British Columbia, N. lat. 57°22′, W. long. 123°55′, provided the materials for the original description of *S. axius* and *Geranocephalus inopinus*. Both these are represented by undamaged, articulated shells occurring in very dark grey, argillaceous limestone. The only other fossil with them is *Ambothyris sublineata;* all occur in a zone 493 to 572 feet below the limestone top. Possibly this top is somewhat higher, stratigraphically, than Ramparts top. Lower in the same formation, there are biohermal bodies faintly outlined; about 1000 feet below formation top, the *Atrypa arctica* fauna occurs. Most of the deposit suggests sedimentation at some depth; on the other hand, there are limestone rubble beds (indicative of penecontemporaneous erosion) in the formation, and the top is said to be fragmental.

The new species named herein were first found in a group of Middle Devonian localities within the mountains, centering round Monkman Lake, British Columbia, N. lat. 50°35′, W. long. 121°5′. One of these, described as 6 miles NNE of Sentinel Peak is 45 miles north-west of Monkman Lake. The rock is black, very argillaceous limestone. Here, *G. inopinus* occurs 160 feet below the limestone top. An unidentified *Stringocephalus* occurs 260 feet below top. *S. chasmognathus* occurs with *Geranocephalus* sp. 370 to 460 feet below top. *Gyroceras canadense*, an accompanier of *S. sapiens* at other places, occurs at 700 feet below top. The fossils are whole and articulated; they occur with *Paracyclas* sp., *Spongophyllum pax*, and cystiphylloid corals.

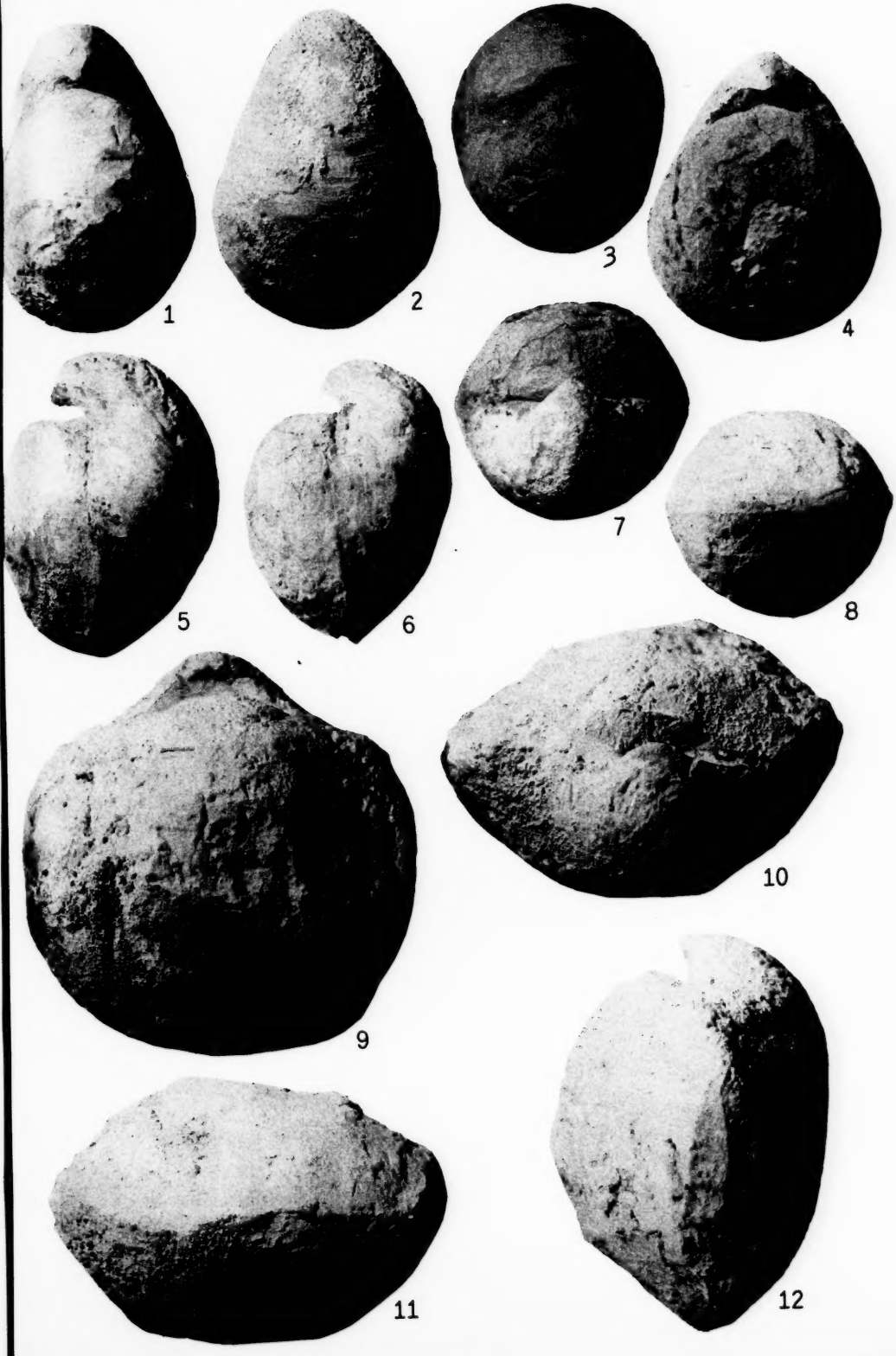
A locality 6 miles east of Sentinel Mtn. yielded *S. axius* and *G. inopinus* between 290 and 390 feet below limestone top. *S. chasmognathus* and *G. inopinus*, 460 to 480 below top. And *S. glaphyrus* and *S. sapiens* (holotype) about 700 feet below top. Among these *S. chasmognathus* is accompanied by *Elytha compacta*, *Spongophyllum pax*, various cystiphylloids and *Alveolites* sp. n. *S. glaphyrus* is accompanied by *Ambothyris sublineata*, *Thamnopora* sp., *Favosites* sp., and (rare) *Clathrodictyon* sp. Lithology and preservation are like the last.

These two localities establish a definite succession pattern among the *Stringocephalus* species, giving them a zonal value. The *axius* or "*burtini*" zone (Warren and Stelck, 1956), formerly including all occurrences of *Stringocephalus*, must now be restricted to the highest part of the interval marked by that genus. *S. chasmognathus* and *S. glaphy*

EXPLANATION OF PLATE 113
All figures ×1

FIGS. *1–8*—*S. glaphyrus*, *1*, holotype, dorsal aspect; *2*, same, ventral aspect; *3*, same, posterior aspect; *4*, paratype 1, dorsal aspect; *5*, holotype, left lateral aspect; *6*, paratype 1, left lateral aspect; *7*, same, posterior aspect; *8*, same, anterior aspect.

9–12—*9*, *S. sapiens*, paratype 1, dorsal aspect; *10*, same, posterior aspect; *11*, same, anterior aspect; *12*, same, left lateral aspect.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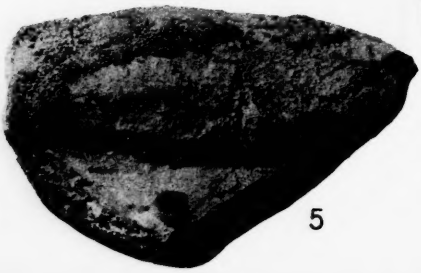

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rus mark, respectively, two lower zones in that interval. It is suggested, therefore, that one may use where possible the finer zoning:

S. axius
S. chasmognathus
S. glaphyrus

or, where not thus divisible, the gross interval may still be termed *Stringocephalus* zone. But as a zonal term *axius* must hereafter be limited. It has appeared that these lines might be read and misunderstood by geological workers in the oil industry unfamiliar with the theory of dissimilar faunas. The essential thought on the evidence here given is that consistent patterns in the stratal occurrence of fossils permit the assumption of correlation. In other words, *chasmognathus* beds, for example, everywhere are of the same exact geologic date.

Of other localities in Monkman Lake region, that 10 miles east of Sentinel Peak has *S. glaphyrus* (holotype) and *S. sapiens* together, about 500 feet below limestone top, in a dark, fragmental limestone in which many shells are broken. A locality 5 miles north-west of the headwaters of Sukunka River lies also 10 to 15 miles northwest of Monkman Lake, and is notable for the occurrence together in dark grey argillaceous limestone of whole specimens of *S. sapiens* and *Gyroceras canadense*, though not in a place that can be related to Ramparts limestone top. A locality 7 miles north-west of Monkman Lake bears *S. chasmognathus* (holotype) and *Elytha compacta* in a dark grey, argillaceous limestone n a condensed section, that is, much thinner than the others, and peculiar in containing sandstones. Finally, a section 5 miles northwest of Fishhook Lake yields *S. glaphyrus* with *Geranocephalus* cf. *inopinus*, cystiphylloid corals, *Spongophyllum pax*, *Thamnopora* sp., *Alveolites* sp., *Spinatrypa* sp., *Warrenella?* sp. and *Paracyclas* sp., from a horizon low in the Middle Devonian though not readily placed in its section. The rock is a dark grey, argillaceous, fragmental limestone including reworked beds. Many of the brachiopods are preserved whole and articulated, but in the areas of reworking, most of the shells are broken and worn.

Throughout the mountain belt of Middle Devonian occurrences, the Stringocephalines occur in fine-grained, black, argillaceous limestone, and black shales. The only departures from this rule are in the cases of broken or worn specimens occurring in reworked beds some of which contain sand and are of a slightly lighter grey color.

SUMMARY OF INTERPRETATION

It has been seen that the *Stringocephalus*-bearing beds occur throughout the MacKenzie River basin of north-western Canada, throughout the area of Elk Point evaporite basin (though not in sediments in any way suggestive of evaporites) and eastward from it to the limits of the outcrops of deposits of Givetian age. They occur in the Rocky Mountains as far south as latitude 54°20′. It seems likely that the *Stringocephalus* beds formerly extended somewhat farther east and north-east than now, that is, through a somewhat greater overlap, subsequently eroded from the Shield. On the other hand,

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EXPLANATION OF PLATE 114
All figures ×1

FIGS. *1–4*—*S. sapiens*, *1*, paratype 1, ventral aspect; *2*, holotype, ventral aspect; *3*, Same, dorsal aspect; *4*, Same, left lateral aspect; the valves are displaced with respect to each other, the brachial valve having been carried in the anterior direction.

5–7—*S. chasmognathus*, *5*, paratype 1, posterior aspect; *6*, holotype, left lateral; *7*, paratype 1, left lateral aspect.

it is scarcely possible that they had any former greater westward extent in Elk Point basin, that is, in the Devonian overlap on the western Alberta axis which includes the Spirit River high or Peace River arch, a paleostructural arch of Devonian time, at its northern end. The possibility of greater extent southward in the Rocky Mountains than that now known is still open, though it seems unlikely that there was ever so great an extent in this direction as to bring the *Stringocephalus*-bearing formation as far south as the main area of Montana.

There is, of course, a "*Stringocephalus*" form recorded from central Nevada and western Utah (Merriam, 1940). Relationships with the north-western Canada occurrences have not been approached.

On the basis of lithology, the western Canada occurrences of *Stringocephalus* are divided into two types which are correlative with geographic position. In the plains region, from Manitoba to the Arctic, the *Stringocephalus* beds are pure to somewhat magnesian, granular, reefal or clastic limestones usually of a light buff color; this is the eastern type. Its position is, at least where it enters the Elk Point basin, between the two thickest evaporites. In the mountain region, including the area of the Imperial Island River No. 1 borehole, the beds are black argillaceous limestone; this is the western type. On the face of it, the contrast is enormous. In the circumstances, the community of fossil species becomes a problem in ecological interpretation which is scarcely discernible, much less soluble, through lithological evidence alone.

The eastern type of occurrence includes, in its best development which is east of the evaporite basin (though it extends, of course, completely across that basin) a profusion of robustly developed reef-builders; it was an environment of luxuriant, shallow-water reef growth. There are in these deposits some calcareous algae, a group that thrives in shallow, even in rough water. The very thick, strong, heavy shells of mollusks and some brachiopods confirms this. The large-scale replacement of spiriferoids by *Atrypa* and *Spinatrypa* indicates shallower depths than the optimum for the former; and the total absence of leiorhynchoids suggests a similar conclusion. The fact of some shells having been broken before deposition points to an origin of the deposit in the region of strong wave action and, by a second inference, shallow water. The same thought is borne out by the confusedly conglomeratic character of much of the limestone, the mollusk and brachiopod shells in it lying in confusion among hollows between coralline heads. Furthermore, there are the calcareous algae; and they provide the only evidence for shallow water independently of argument based on wave influence.

On the other hand, the excellent preservation of most of the shells (particularly the mollusks) interferes with one's thinking that they were exposed to any considerable wave action. Crinoid stems with great numbers of columnals still articulated seem to prove deposition at a quiet depth, though crinoid heads are almost unknown, and perhaps that points to a limit. The occurrence of a sponge suggests a depth where wave disturbance was at most little. Finally, the fact of many or most of the bivalve shells being still articulated confirms the other suggestions in this paragraph, and stands stubbornly against the conclusions in the last.

Conflicting pieces of natural evidence do not necessarily invalidate each other: in the *Stringocephalus*-bearing deposits, factual indications of both great shallowness and of considerable depth, though mutually contradictory, may still be rationally reconcilable, for it is quite possible in nature for contrary indications to become mixed. Before understanding of them is possible, they require analytical separation. The Middle Devonian of western Canada is full of evidence of variation in conditions: repeated deep subsidence in evaporation environments, intervals of unfossiliferous red-bed formation (whatever they mean), and combinations of open sea, reef-building, and deposition of fairly ordinary fossiliferous sediments at very various depths. Here, very plainly, is great variation. May there not, then, have been considerable variation of conditions of sedimentation even within the shorter time marked by the apparently continuous carbonate deposition of the *Stringocephalus* beds? If this environment

varied repeatedly through a shallow-to-deep cycle of diastrophism, even through an irregular cycle, with the products of shallow-sea environments becoming preserved through the very process of deepening, the observed mixing of apparently conflicting evidence is not too unexpectable.

The western or Rocky Mountain type of occurrence differs from the other most evidently in the color of the deposits—they are invariably dark grey to almost black. They are also considerably thicker, and in composition dominantly argillaceous. These three are very great differences. On the other hand, there are some resemblances: like the eastern, the western type presents mutually contradictory kinds of evidence bearing on depth of deposition and other environmental conditions. There is, for instance, the dark color. This is usually taken to indicate a silled basin comprising an euxinic environment. But where it also includes an abundance of healthy-appearing open-sea animals, it can not be truly euxinic, and, though perhaps silled, can not well have been shallowly so.

Furthermore, it is noteworthy that the stromatoporoids are much less common in the mountain sections, and the corals are far from abundant. None the less, corals of all kinds—*Disphyllum*, *Hexagonaria*, cystiphylloids (ceratoid), *Favosites*, *Thamnopora*, *Alveolites*—occur there, as though in defiance of environment. *Thamnopora* is the one that comes near to abundance: it is amazing to observe great numbers of them not only in limestone but in black shale beds. Some parts of the mountain sections have been described as "reefal" and "almost reefal," but these are not the particular beds that contain stringocephalines. Spiriferoids (e.g. *Elytha*) are common, as are the smooth Spiriferacea (e.g. *Ambothyris*), but *Atrypa*, so numerous in the eastern type, is rare. This seems to indicate somewhat deeper water in the western.

Degree of preservation offers contradictory evidences. Most of the fossils are quite unworn, most of the bivalves have their shells still articulated as in life. One extreme example may be mentioned: the holotype of *S. axius*, though not fully recovered in the collecting, was none the less the whole, articulated shell with its valves somewhat gaping—making it the more vulnerable to disarticulation by undulatory oscillation in the Devonian sea. The evidence indicates the extreme minimum of water motion necessary to bring in the terrigenous material and drop it. On the other hand, some beds, particularly those nearer the base of the Devonian, are rubbly and sandy, and contain about as many broken and disarticulated shells as whole ones. The evidence of erosion in shallow water is unmistakable; nevertheless, it is erosion penecontemporaneous with deposition.

Mention of arenaceous constituents in the lower beds, and argillaceous all through the mountain Middle Devonian brings up the problem of the origin of this terrigenous waste. Sand at the base of the Devonian could be visualized as having been transported from the east, though it is an unlikely source in view of geographical complications in the form of the Elk Point basin and an elevated axis on the west side of it which it would be necessary to cross. On the other hand, the argillaceous material which occurs all through the mountain Middle Devonian could not well have been derived from the east except in minor quantities from the erosion of the West Alberta axis. The major source of the sedimentary material could only have been an axis the present-day traces of which lie west of the Rocky Mountains.

The Rocky Mountain Middle Devonian sea-way resembled the other in being somewhat shallow; it was distinctive only in receiving much *argillaceous* material and in depositing mainly *dark to black* sediments. An unperceived causal relationship between these two facts is suspectable.

PALEONTOLOGY

Attention must now be given to exact discrimination of the one existing North American form of *Stringocephalus*, namely *S. axius*, and the description of three new species, *glaphyrus*, *sapiens* and *chasmognathus*. These four forms appear to be very distinct from each other, though there is considerable variability in some of them; they seem quite different from the foreign species, none of which the writer has been able to recog-

nize among material collected on this continent. The opportunity of distinguishing them is a valuable one: there has long been a difficulty in demonstrating the existence of distinct North American species; but now that it appears that European names have been applied on this continent without real discrimination, there is a necessity to achieve the object of displacing them.

Phylum BRACHIOPODA
Superfamily TEREBRATULACEA
Family STRINGOCEPHALIDAE
Subfamily STRINGOCEPHALINAE

Medium to very large, terebratuloid brachiopods, with smooth, endopunctate shells, having a very large cardinal process.

Genus GERANOCEPHALUS Crickmay
1954

Remarks.—There appear to be more than one form of this genus. For instance, in the talus at certain localities, a form with an almost catacline interarea has appeared. However, *G. inopinus* is found in most of the sections at various horizons with the new species of *Stringocephalus* which it exceeds considerably in the difficulties of its study. It seems best, until more abundant material is available, and from definite localities and stratigraphic positions, to make no attempt to distinguish from *G. inopinus* any of the expected new forms. Even without distinction, any form of *Geranocephalus* is a good guide: the genus appears to be, as to range, a constant companion of *Stringocephalus;* and its characteristics are quite unmistakable. Where it is found alone, it may still be taken as indicating part of the *Stringocephalus* beds. The genus is distinctive in having median septum in neither valve. Correction of the original or type description would describe the beak as straight (using Cloud's term).

Genus STRINGOCEPHALUS
Defrance 1825

STRINGOCEPHALUS GLAPHYRUS n. sp.
Pl. 113, figs. 1–8; text-figs. A1–A6

Description.—Shell, small, rotund or globose. Valves of equal convexity, of somewhat variable conformation. Shell substance, thick. Surface, smooth, glassy.

Pedicle valve, pyriform in outline, roundly inflated posteriorly. Beak, small, trim, very strongly incurved. Interarea, very small, curved. Delthyrium, small. Deltidium, concave, concealed by incurved beak, pierced by an oval foramen that is large for the size of the shell and is placed high up under the beak. Cardinal margin, concealed by opposing valve. Hinge teeth, strong, well-formed, supported by a ridge of callus within the shell. Median septum, thick and obtuse in apical region, maintaining thickness but becoming sharp-edged through umbonal region, thin and acute toward anterior, about 75 to 80 percent of length of valve.

Brachial valve, round in outline, semiglobe-shaped. Beak, inevident. Hinge plate, strong, regular, with well-formed sockets, merging into suspended crural plates. Cardinal process, short, deeply divided, with widely diverging arms of variable form and development. Median septum, 35 to 40 percent of length of valve, rather low throughout, separated from cardinal process and from crural plates at a place considerably posterior to that at which separation takes place in other forms—(in transverse serial sections prior to appearance in section of cardinal process, or, in other words, becoming low and separated from cardinal apparatus at an early stage).

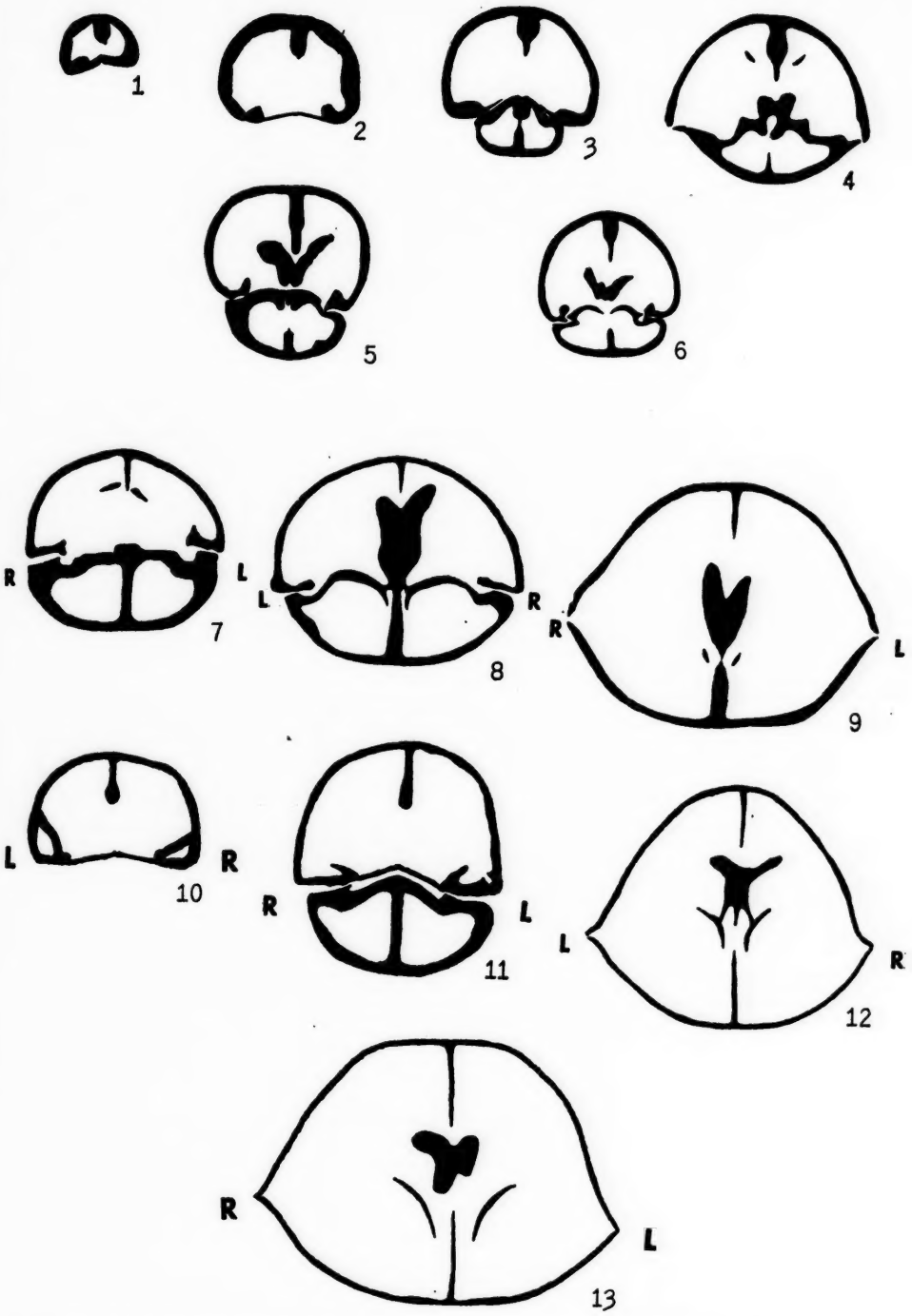
Dimensions.—Length of pedicle valve, 74 mm.; length of brachial valve, 39 mm.; width, 40 mm.; depth (valves together), 35 mm.

Occurrence.—Holotype and paratypes 2 and 3 from *glaphyrus* zone in a short section representing the lower part of the Middle Devonian, with *S. sapiens*, 10 miles east of Sentinel Peak. Paratypes 1 and 4, from 5 miles northwest of Fishhook Lake, B. C. The species occurs also in lower part of Ramparts formation, 200 feet below *S. chasmognathus*, of the section 6 miles east of Sentinel Mtn.

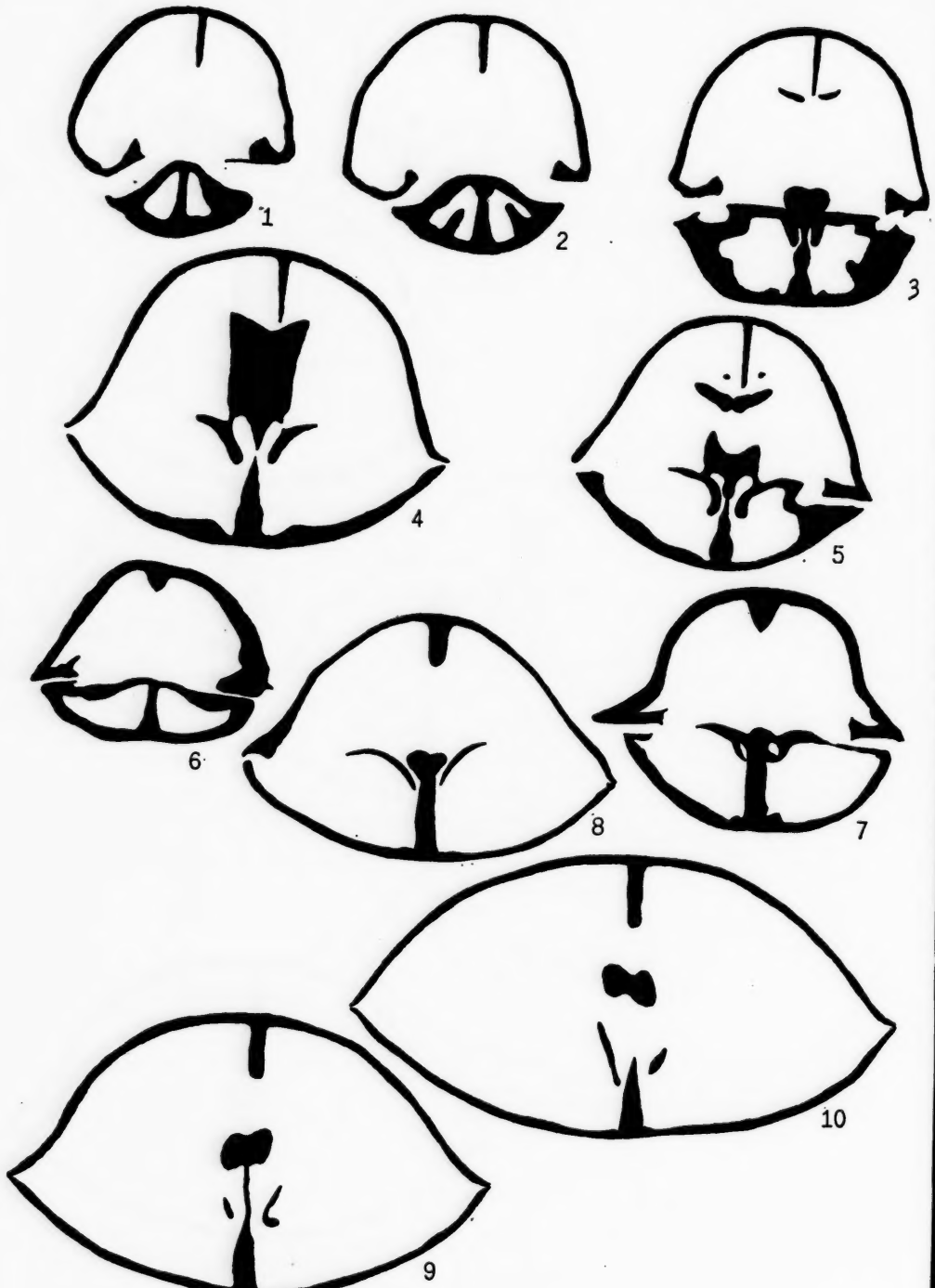
Name.—Descriptive, gleaming.

STRINGOCEPHALUS SAPIENS n. sp.
Pl. 113, figs. 9–12; pl. 114, figs. 1–4; text-figs. A7–A13, B1–B5

Description.—Shell, of medium size, very variable in form and development. Valves,



TEXT-FIGS. *A1–A13*—All figures are transverse sections. *A1–A4*, *S. glaphyrus*, paratype 2; *A5*, *S. glaphyrus*, paratype 3; *A6*, *S. glaphyrus*, paratype 4; *A7–A9*, *S. sapiens*, holotype; *A10–A13*, *S. sapiens*, paratype 1. All are natural size.



TEXT-FIGS. *B1–B10—B1–B5, S. sapiens*, paratype 2; *B6–B10, S. chasmognathus*, paratype 4. All are natural size.

of nearly equal convexity. Shell substance, thin. Surface, smooth.

Pedicle valve, roundish in outline, moderately convex. Beak, gross, somewhat incurved. Interarea, large, uneven of surface. Delthyrium, large. Deltidium, narrowly triangular, notably concave, pierced by a small, round foramen located rather close to the beak. Cardinal margin, submerged under opposing valve. Hinge teeth, well developed, supported by short, diverging dental lamellae and much internal callus. Median septum, low and obtuse in apical region, thick and acute in umbonal region, thin toward anterior, about 60 to 70 percent of length of valve.

Brachial valve, roundish in outline, moderately convex. Beak, obtuse, low. Hinge plate, strong, regular, with deep sockets, merging into large, curved, suspended crural plates. Cardinal process large, broadly spatulate, fairly deeply divided, with diverging extremities, supported not merely by the septum but by a lateral process on each side connecting it with the crural plates. In serial transverse sections, the lateral processes persist, either whole or broken, after the connection with the septum is severed. Median septum, stout, of variable form, of very variable length of 35 to 75 percent of length of valve, of variably weak or strong connection to cardinal process. Most, but not all, examples exhibit strong internal ridges running radially in apical to umbonal region.

Dimensions.—Length of pedicle valve, 68 mm.; length of brachial valve, 58 mm.; width, 68 mm.; depth (valves together), 49 mm.

Occurrence.—Holotype from *glaphyrus* zone in lower part of Middle Devonian section, with *S. glaphyrus*, 680 feet below limestone top, or 200 feet below *S. chasmognathus*, six miles east of Sentinel Peak. Paratype No. 1, from lower part of Middle Devonian limestone, with *S. glaphyrus*, 10 miles east of Sentinel Peak. Paratype No. 2, with *S. sapiens* var., *S. glaphyrus*, *Elytha* sp., *Gyroceras canadense*, *Favosites* sp. n., in a short Middle Devonian section 5 miles northwest of the headwaters of Sukunka River, B. C. (It may be noted that 6 miles north-north-east of Sentinel Peak, *G. canadense* occurs 700 feet below Ramparts top, and 300 feet below the occurrence of *S. chasmognathus.*)

Name.—Traditional, *strix sapiens.*

STRINGOCEPHALUS CHASMOGNATHUS sp. n.

Pl. 114, figs. 5–7; pl. 115, figs. 1–6; text-figs. B6–B10, C1–C9

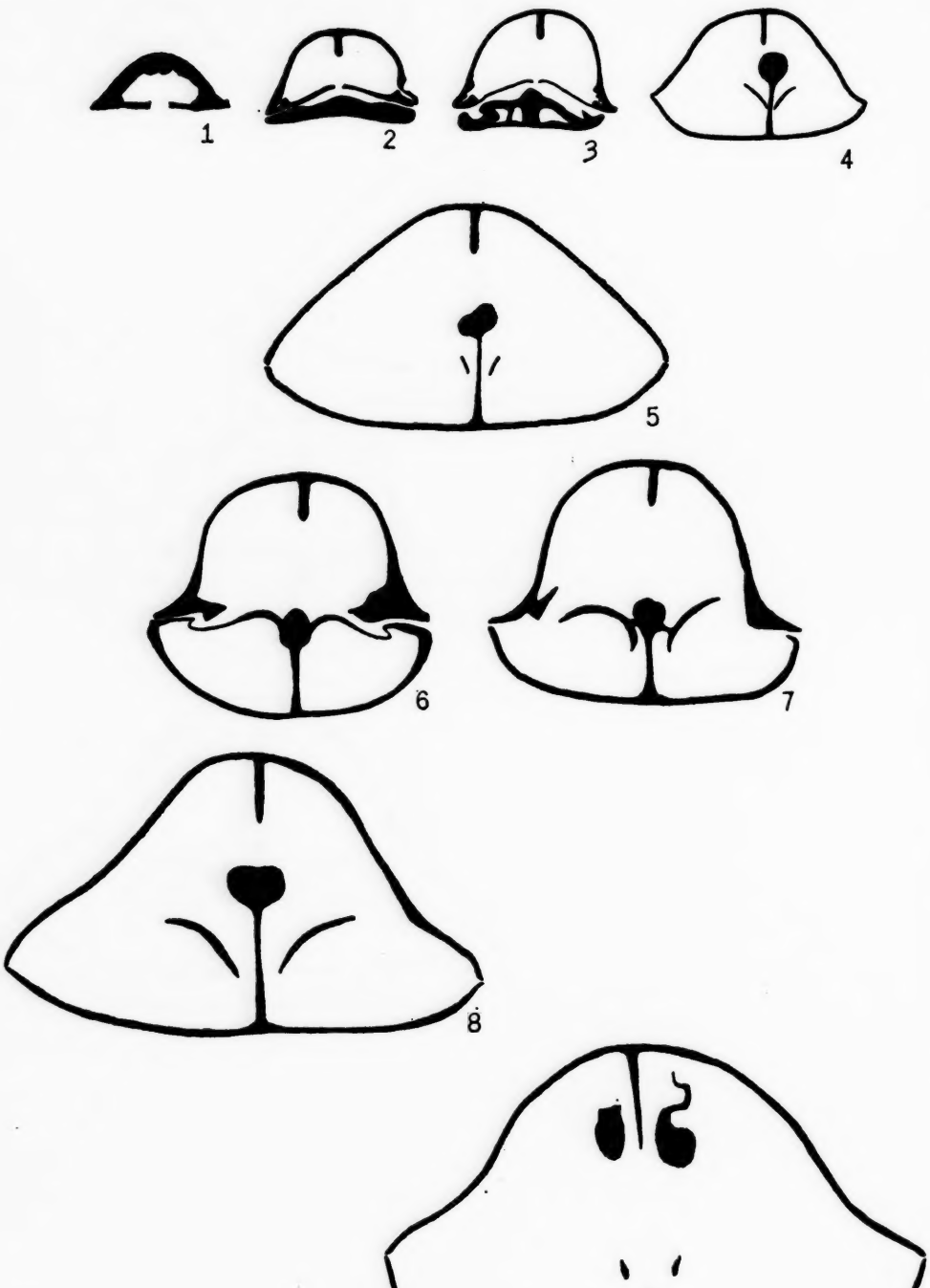
Description.—Shell, large, little inflated. Valves, nearly equal, varying much from one individual to another. Shell substance, thin. Surface, smooth.

Pedicle valve, gently convex. Beak, prominent, suberect. Interarea, broad, flattish, approaching catacline. Delthyrium, large, broadly triangular. Deltidium, pierced by small, roundish foramen. Cardinal margin, submerged between valves. Hinge teeth, strong, but amorphous and irregular in development, supported by strong callus only. Dental lamellae, early obsolescent. Median septum, low in apical region, becoming prominent though remaining thick and blunt-edged through umbonal region, becoming acute in anterior region, totalling about 80 percent of length of valve.

Brachial valve, with prominent, wide umbo. Disk, flattish in anterior part. Beak, inevident. Hinge plate, thin, regular, with well-formed sockets, merging imperceptibly into broad, curved, diverging, freely suspended crural plates. Cardinal process, very long, roundly rod-like, straighter than in other species, directed mainly anteriorly as well as ventrally, divided only in the last fifth of its length, the dividing lobes being laterally compressed and ventrally attenuated to a ribbon-like edge; in some specimens, the extremities touch the opposing valve. Median septum, strong, 60 to 80 percent of length of valve, very high posteriorly, and persistently connected with the cardinal process.

Dimensions.—Length of pedicle valve, 76 mm.; length of brachial valve, 67 mm.; width, 88 mm.; depth (valves together), 44 mm.

Occurrence.—Holotype and paratypes 1, 2 and 3 from *chasmognathus* zone in a Middle Devonian section seven miles north-west of Monkman Lake, British Columbia. The occurrence is 260 feet below the top of the



TEXT-FIGS. *C1–C9—C1–C4, S. chasmognathus*, paratype 3; *C5, S. chasmognathus*, paratype 1; *C6–C9, S. chasmognathus*, paratype 2. All are natural size.

TEXT-FIGS. *D1–D3—D1, S. axius*, topotype, transverse section of central region; *D2*, same, 10 mm. anterior to fig. D1; *D3*, same, in plane of commissure; shows paired abutting portions of posterior margin of brachial valve, paired crural plates showing bosses, crural process and median septum. Two-thirds natural size.

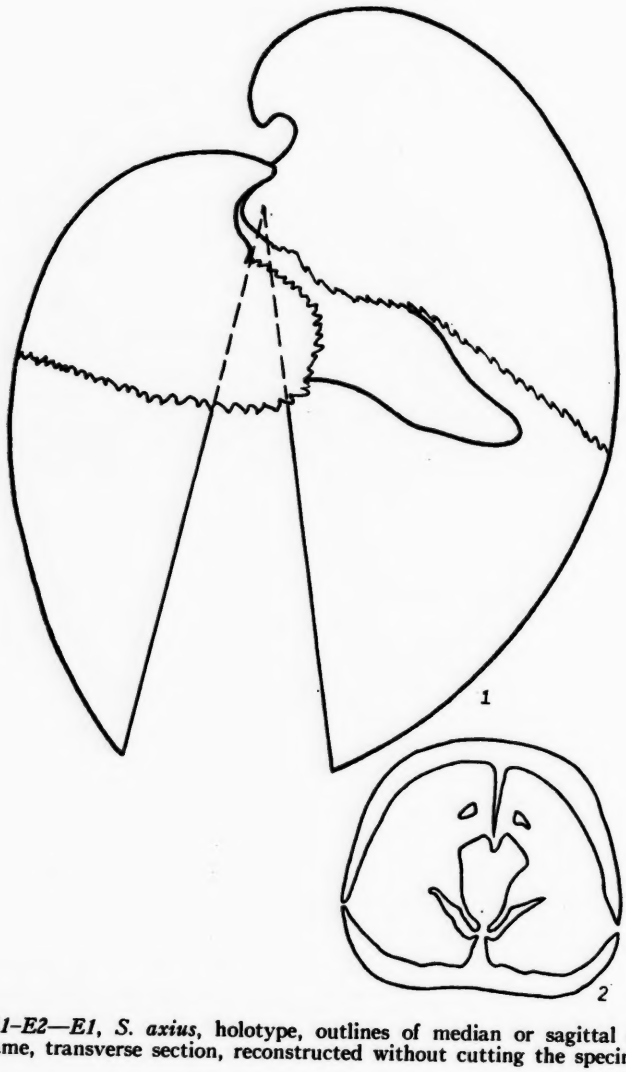
Ramparts limestone equivalent. Paratype 4 from 450 feet below Ramparts top, or 230 feet below center of occurrence of *S. axius*, at a section 6 miles east of Sentinel Mtn., B. C. Species was found also at 360 to 460 feet below Ramparts top 6 miles north-northeast of Sentinel Peak.

Name.—Descriptive, gaping jaws.

Remarks.—From 6 miles east of Sentinel Mtn., and elsewhere, a dwarf variety with both valves almost flat, and catacline interarea, was obtained. The form suggests a species of *Geranocephalus*, but is quite distinct. If more specimens are ever obtained, it will be possible to describe and name it as a species.

STRINGOCEPHALUS AXIUS Crickmay 1954
Text figs. D1–D3, E1–E2

Remarks.—When this species was described (Crickmay, 1954), it was insufficiently realized that variability among specimens of North American brachiopods referable to the genus *Stringocephalus* might indicate the existence of distinct and at closest little related lineages and non-coeval developments. The tendency to lump all such forms together—even to list them by a



TEXT-FIGS. *E1–E2—E1*, *S. axius*, holotype, outlines of median or sagittal section, in part restored; *E2*, same, transverse section, reconstructed without cutting the specimen. Two-thirds natural size.

European name—is an old one and a persistent one (Warren and Stelck, 1956, p. 8, pl. V, VI). The recognition of distinct species is achieved herein, but the mere naming of other forms leaves *S. axius* less recognizable. To this, there is only one remedy, and that is to re-examine the type description.

In most of its terms, the original description of *S. axius* is sufficiently apt until one attempts to distinguish it from *S. sapiens*, for instance, which has a variably thick shell when young but becomes thin, and hence at some stages is not easily distinguishable from *axius*. The deficiency in description of *axius* centers round the internal structures. The dorsal hinge plate, for instance, is not so much supported by crural plates as supporting them, for it merely merges into the crural plates which are suspended from it and from the median septum.

Furthermore, the crural plates of *S. axius* are highly distinctive in being marked on their exposed faces with a central boss which was no better than imperfectly illustrated in plate 3, figure 2, of the type description. Again, the cardinal process itself ought to be noted as supported through much of its length by the median septum which is strong and persistent; the process bears an acute, median ridge on its posterior surface.

The transverse sections given with the type description are of immense interest in illustrating a perfectly preserved, very immature specimen, but they do not show any of the character of the mature shell. This defect is remedied in the accompanying illustration which has been made by reconstruction, without sectioning, from the holotype. Two specimens of this species from another locality were sectioned to amplify the illustrations. It will be instructive to compare the new illustrations with plate 2 of the 1954 paper. It may here be noted, and with emphasis, that the internal structures are among the best distinctions in Stringocephalidae. The figure of the outline of the shell from lateral viewpoint, given herein, embodies a correction of drafting applied to the large 1954 figure.

Occurrence.—This was originally listed as from "Ramparts" formation, 572 feet below top, at Redfern Lake, British Columbia, 57°20′ N. lat., 124° W. long. In view of newer findings, the depth below formation top appears excessive, and may well indicate that the limestone top is higher, stratigraphically, than true Ramparts top. Hence, the position of *S. axius* may be little more than 300 below Ramparts top equivalent.

S. axius occurs with *Geranocephalus inopinus* in the section 6 miles east of Sentinel Mtn., B. C., from 300 to 380 feet below top of Ramparts limestone. In the section 6 miles north-north-east of Sentinel Peak, *G. inopinus* occurs 160 feet below Ramparts top, and *Stringocephalus* sp. (probably *axius*) at 260 feet. The centers of these occurrences are, respectively, 230 and 200 feet above the middle of *chasmognathus* occurrence, and 360 and 500 above *glaphyrus*. No form similar to *S. axius* has ever been seen in these lower zones.

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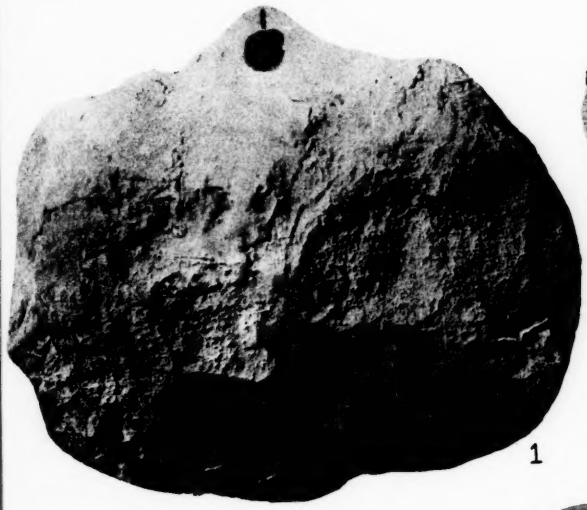
MANUSCRIPT RECEIVED OCTOBER 1, 1959.

(*Explanation of* PLATE 115 *on next page.*)

EXPLANATION OF PLATE 115
All figures ×1

FIGS. *1–6*—*S. chasmognathus*, *1*, holotype, natural size, dorsal aspect; *2*, paratype 1, ventral aspect; *3*, same, dorsal aspect; *4*, holotype, ventral aspect; *5*, same, anterior aspect; *6*, same, posterior aspect.



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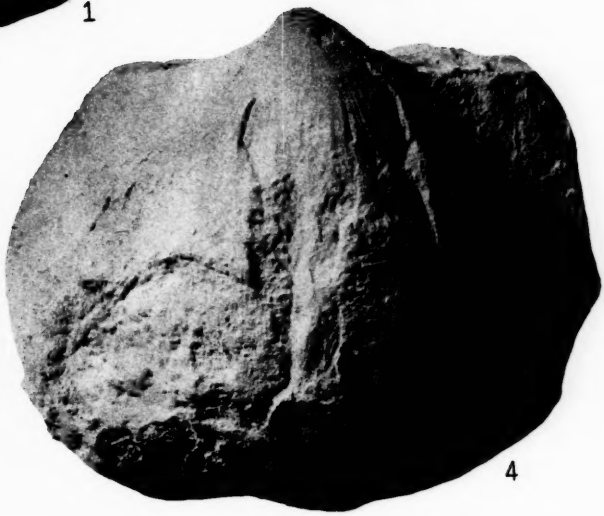

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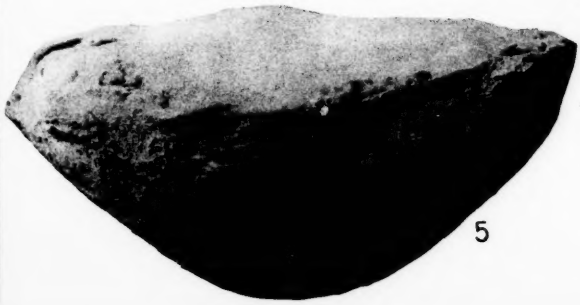

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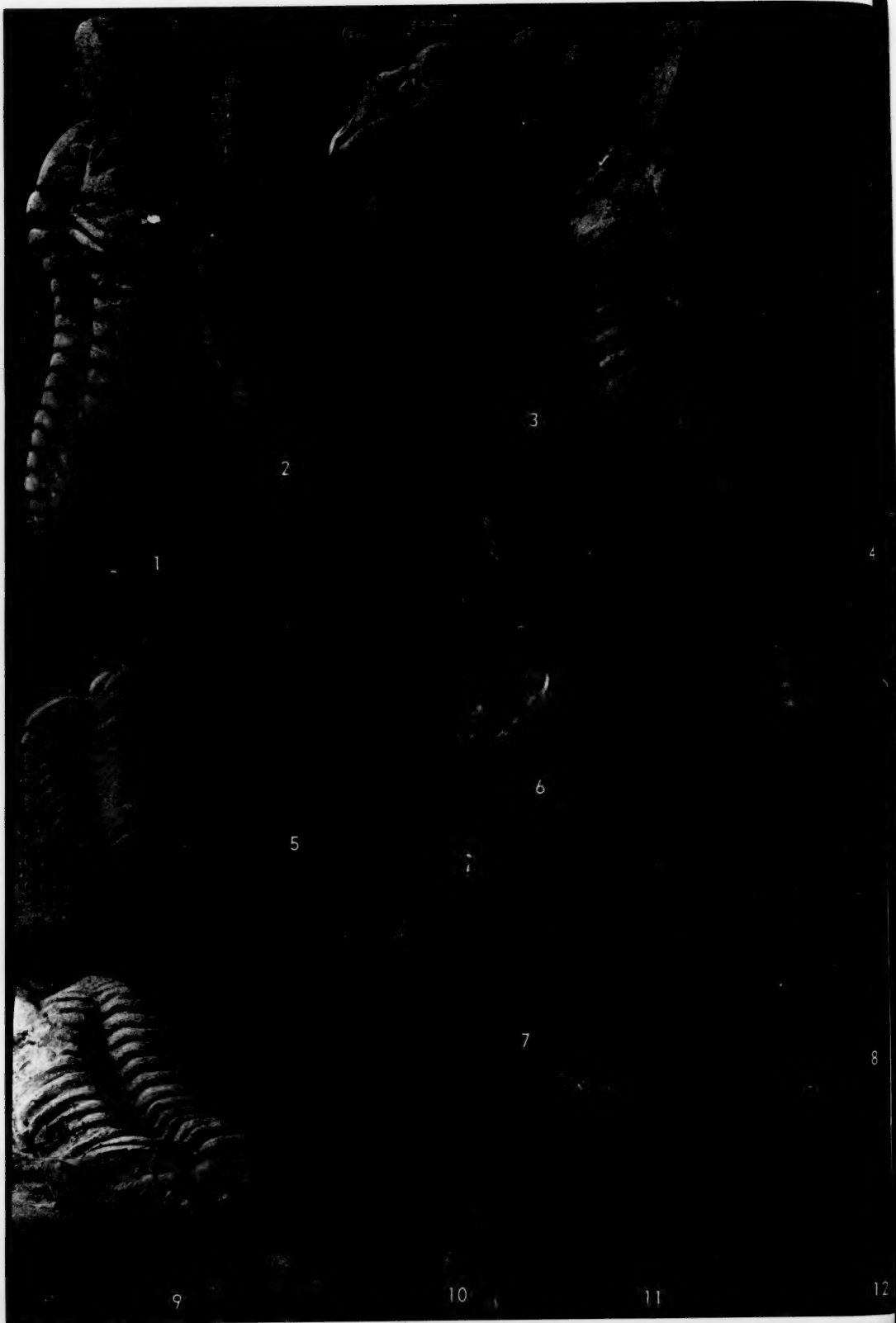
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JOURNAL OF PALEONTOLOGY, V. 34, NO. 5, P. 891–895, PL. 116, SEPTEMBER, 1960

SPATHACALYMENE, AN UNUSUAL NEW SILURIAN TRILOBITE GENUS

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ABSTRACT—*Calymene nasuta* Ulrich, from the Middle Silurian Osgood formation of southeastern Indiana, is redescribed on the basis of type material from the U. S. National Museum and a new, nearly complete specimen. It is characterized by the possession of a spatulate anterior border process and is designated the type species of *Spathacalymene* n. gen.

INTRODUCTION

IN 1879 E. O. Ulrich (1879, p. 131–134) described and illustrated a reconstruction of a new species of calymenid trilobite, *Calymene nasuta*, found in the " . . . lower beds of the Niagara Group, at Osgood, Ripley county, Indiana." The species was unusual in the possession of a large spatulate process developed from the anterior border. J. F. Pompeckj (1898, p. 242–243) transferred the species to *Calymenella* Bergeron. R. S. Bassler (1915, p. 170) retained the species in *Calymenella* and the cotypes at the U. S. National Museum are so labelled. *Calymenella*, however, is a homalonotid whereas *C. nasuta* is a calymenid. *C. nasuta* is, in fact, sufficiently distinctive to merit a new generic designation for which the name *Spathacalymene* is here proposed.

Ulrich's original description and illustration was apparently based on the seven cotypes now bearing U. S. National Museum catalog number 41871. The present redescription is based mainly on two of these specimens (pl. 116, figs. 2,3,6,7,10–12) and on a new specimen collected by Mr. John Cutler, Cincinnati, Ohio (pl. 116, figs. 1,4,5,8,9) who generously loaned it to the writer.

Mr. Cutler's specimen is from a quarry in the Middle Silurian Laurel limestone, 0.8 miles due east of Napoleon, Indiana. Drainage ditches dug in the quarry floor have exposed about 18 inches of the underlying Upper Osgood shale which is also of Middle Silurian age. This is a gray calcareous shale containing a few interbedded lenticular greenish-gray fine-grained argillaceous limestones. The trilobite was collected from the material excavated from the drainage ditches and is inferred to be from one of the interbedded limestones of the Upper Osgood shale.

ACKNOWLEDGMENTS

The writer wishes to thank Mr. John Cutler, Cincinnati, Ohio for the loan of his specimen of *Spathacalymene;* Dr. G. Arthur Cooper, U. S. National Museum, for kindly making available Ulrich's type specimens; and Prof. H. B. Whittington, Museum of Comparative Zoology, Harvard University, with whose encouragement and guidance this paper was prepared.

EXPLANATION OF PLATE 116

FIGS. 1–12—*Spathacalymene nasuta* (Ulrich), 1879. *1,4,5,8,9,* Right lateral, dorsal, postero-dorsal, antero-dorsal, and right anterior dorso-lateral views. Osgood formation, Napoleon, Indiana. John Cutler Collection, ×1; *2,3,6,7,* Left lateral, dorsal, antero-dorsal, and left anterior dorso-lateral views. Osgood formation, Osgood, Indiana. Lectotype, U.S.N.M. 41871, ×1.5; *10–12,* Right lateral, ventral, and dorsal views. Osgood formation, Osgood, Indiana, U.S.N.M. 41871, ×1.

SYSTEMATIC PALEONTOLOGY

Family CALYMENIDAE Burmeister, 1843
Subfamily CALYMENINAE Burmeister, 1843
Genus SPATHACALYMENE, n. gen.

Type species.—Here designated, *Calymene nasuta* Ulrich, 1879, from the Osgood formation, Osgood, Indiana.

Diagnosis.—Papillate calymenid trilobite characterized by great but variable development of U-shaped or spatulate process from anterior border, very deep preglabellar furrow, large rostrum with open V-shaped anterior edge and unknown posterior edge, distinct flattening of tops of axial and pleural thoracic lobes, twelve (?) or thirteen thoracic segments, pygidium with five axial rings and four pleural furrows, the latter extending only two-thirds of way to ventral edge of pleurae, very faint interpleural furrows on inner parts of pleurae only.

Occurrence.—Known only from the Osgood formation, Middle Silurian, southeastern Indiana.

Comparisons.—Ulrich placed his species in the genus *Calymene* but it differs from the genotype species *C. blumenbachi* in nearly all the items mentioned in the generic diagnosis. In contrast to *S. nasuta, C. blumenbachi* has no spatulate anterior process, the rostral suture parallels the broadly convex anterior edge of the anterior border, the crests of the axial and pleural thoracic lobes are rounded, the pygidium has six axial rings and five pleural furrows, its pleural furrows extend to the ventral edge, interpleural furrows are absent, and the pygidium is proportionately longer and narrower and has a wider axial lobe.

Pompeckj (1898, p. 242–243) transferred Ulrich's species to *Calymenella* Bergeron and ranked *Calymenella* as a subgenus of *Homalonotus* Konig. *Spathacalymene* has a characteristic calymenid glabella and there seems no justification for classifying this species with homalonotids. In *Homalonotus* the glabella is flattened, has less conspicuous glabellar furrows and lobes, and no deep preglabellar furrow; the shape of the anterior border, the course of the facial sutures and the outline of the rostrum is quite different.

Reedocalymene Kobayashi and *Calymenesun* Kobayashi, calymenids having a spatulate anterior projection and an anterior spine respectively, differ from *Spathacalymene* in the form and origin of these processes and in details of glabellar and pygidial morphology.

Function of anterior border process.—Anterior spines and processes of various kinds are present in several families of trilobites. In addition to the two genera of calymenid and one genus of homalonotid trilobites mentioned above, certain genera of raphiophorids, alsataspidids, hapalopleurids, emmerichellids, marjumiids, remopleuridids, asaphids, dalmanitids, calmoniids, and phacopids are also known to develop such structures. Anterior projections arise in at least four different ways; as expansions of the anterior end of the glabella, e.g. *Ampyx* and *Lonchodomas;* as expansions of the anterior border, e.g. *Spathacalymene;* as expansions of frontal areas, e.g. *Calymenesun* and *Hapalopleura;* and as expansions of the anterior parts of the free cheeks, e.g. *Neoprobolium* and *Paracalmonia.* In some cases the free cheeks expand to form only part of the process, e.g. *Ectenaspis* and *Nasocephalus.* The facial sutures parallel the forward expansions in the last two genera. In *Spathacalymene* the rostral suture bends forward along the under surface of the process so as to produce a rostrum with a rounded V-shaped anterior margin. In an undescribed Siluro-Devonian phacopid from Maine, in the collection of A. J. Boucot, the rostral suture produces a rostrum with a U-shaped anterior margin.

The outline and profile shape of the processes varies considerably from species to species and one may observe long slim spines, e.g. *Ampyx;* flattened spines variously branched terminally, e.g. *Neoprobolium;* long spatulate forms, e.g. *Spathacalymene;* and short V-shaped forms, e.g. *Nasocephalus.*

None of the processes is known to be articulated with the carapace. They are more or less rigid outgrowths which form a unit with the anterior border, the anterior lobe of the glabella, a frontal area, or combinations of these.

Genal spines may or may not be present in

process-bearing species; of the genera mentioned genal spines are prominently developed in *Neoprobolium*, *Nasocephalus*, *Hapalopleura*, *Ampyx*, and *Lonchodomas*.

The independent development of such processes of different forms and origins in unrelated lines of trilobites and at different times suggests the possibility that they are adaptational features. As such they might be regarded as analogous structures, i.e. similarly functioning organs or structures of diverse origins. To determine what function or adaptational advantage they may have had is a difficult matter.

The presence of anterior processes, like the presence of filamentous antennae (Snodgrass, 1952, p. 8), seems to preclude the possibility that these genera were burrowers in bottom mud as has been suggested for some trilobites. None of them is excessively spiny and for this reason they cannot be logically included with those trilobites thought to be swimmers and floaters in near surface waters. In all probability they swam close to the bottom and scavenged detritus from muddy and sandy bottoms.

If, as suggested by Whittington (1956, p. 185–186) many trilobites rested on the ventral edges of their cephala while feeding, long genal spines would tend to provide added stability in this position and aid in keeping the posterior part of the body slightly off the sea bottom with minimum activity on the part of the animal. It is apparent that in many cases genal spines alone are adequate for this purpose. Where genal spines are absent, however, anterior processes might act as counterweights tending to keep the posterior part of the body off the bottom during feeding or, as has sometimes been suggested, to serve a similar function during swimming. Where both genal spines and anterior processes are present they might both contribute to general stability. Spines developed from the anterior part of the glabella might be even more effective as counterbalances than those developed from areas lower on the cephalon. Anterior spines in such small genal spine-bearing forms as *Ampyx* may also prevent the individual from being overturned by currents or predators. This function seems to be less probable for large forms like *Neoprobolium*.

SPATHACALYMENE NASUTA (Ulrich), 1879
Pl. 116, figs. 1–12

Calymene nasuta Ulrich, 1879, p. 131–134, figs. 1–3.

Calymenella nasuta (Ulrich). Pompeckj, 1898, p. 243; Bassler, 1915, p. 170.

Type specimen.—Lectotype here designated is that specimen illustrated by Ulrich (1879, fig. 1) and in this paper (pl. 116, figs. 2,3,6 and 7) and bearing U. S. National Museum catalog number 41871; this is the only complete specimen in the museum collection. Mr. Cutler's specimen (pl. 116, figs. 1,4,5,8 and 9) is in his private collection.

Other specimens.—The U. S. National Museum collection numbered 41871 contains seven items. In addition to the complete specimen designated the lectotype, it contains one partial cranidium with anterior process cemented in place, here illustrated on pl. 116, figs. 10–12; one large, badly flattened and eroded incomplete cephalon with anterior process; one incomplete cranidium lacking anterior process; two isolated anterior processes lacking rostral plates; and one badly eroded isolated pygidium.

Description.—Outline, excluding U-shaped anterior process, elongate oval, becoming broader anteriorly. Longitudinal profile sinuous. Dimensions of the Cutler specimen, pl. 116, figs. 1,4,5,8 and 9 are as follows: overall sagittal length 91 mm., sagittal length of cephalon 32 mm., length of glabella 16 mm., length of thorax 46 mm., and length of pygidium 13 mm., all uncorrected for curvature. Breadth of widest part of cephalon 52 mm., breadth of widest part of pygidium 22 mm. Height at occipital ring 26 mm., height at anterior edge of pygidium 15 mm.

Cephalon, excluding U-shaped anterior process, semi-circular in outline. Anterior border forming prominent spatulate U-shaped anteriorly projecting process, designated "proboscis" by Ulrich. Process broadly rounded anteriorly but with sides subparallel to divergent posteriorly and continuous with lateral borders of cephalon. Surface of process stands high anteriorly and curves downward posteriorly toward preglabellar furrow; process flatly convex in

transverse section. Exoskeleton continuous over anterior part of ventral surface of process. Tip of process missing from lectotype.

Glabella parabolic in outline and convex sagittally and transversely, standing higher than cheeks and extending 4 mm. forward beyond anterior edge of cheeks. Surface of glabella slopes downward forward so that anterior lobe is suspended and partly concealed in space formed by deep preglabellar furrow. Glabella composed of large frontomedian lobe, small elliptical anterior lateral glabellar lobes and successively larger middle and posterior lateral lobes. Glabella slightly narrower across occipital ring than across posterior glabellar lobes. Glabella as a whole narrows forward but fronto-median lobe expands forward. Two posterior pairs of lateral lobes set off from median lobe by broad shallow furrows paralleling axial furrows and thus convex independently of median lobe. Axial furrows continuous with preglabellar furrow and deep around anterior and posterior lateral lobes but very shallow around middle lateral lobe as a result of presence of a projection, or buttress, extending lobe-ward from fixed cheek. Buttress is met by lobe to produce papillate condition. Axial furrows appear to be continuous with occipital furrow but this may be due to excess scraping during preparation. As a result a low ridge is present in posterior continuation of axial furrow. Ridge joins occipital ring to cheek and another such ridge joins it to posterior border.

Eye lobe small, 5 mm. long, rising about 2 mm. above surface of genal regions, located opposite and 4 mm. out from middle lateral glabellar lobe. Eye surface semicircular in outline with eye surrounded by narrow but clearly marked furrow in free cheek. Fixed cheek, in profile, parallels forward downward curvature of glabellar surface but, due partly to deformation, free cheek slopes vertically antero-laterally or is overturned. Left free cheek, most of fixed cheek, and left lateral cephalic border forward to beginning of projection of anterior border missing in Cutler specimen. All these features well preserved in lectotype. Right fixed cheek of Cutler specimen complete and free cheek still essentially in place but moved backward slightly so as to leave 1 mm. space between inner edge of eye surface and outer edge of palpebral lobe. Right fixed and free cheeks of lectotype not preserved.

Facial suture outlines inner edge of eye surface with posterior branch curving laterally then postero-laterally toward genal angle. Suture cuts posterior border of cephalon at genal angle. Suture proceeds anteriorly from eye directly forward and downward across border. Ulrich's description of position of frontal, or rostral, suture (1879, p. 133) seems misleading. He says, "Frontal suture passing from the intersection of the facial suture and the anterior margin on one side, *upward on the front face of the proboscis* to a point about midway the length of the same where it bends at a right angle and proceeds to the intersection of the facial suture on the other side" (italics mine). Suture actually appears on ventral surface of "proboscis" and marks anterior edge of rostrum. Rostral suture forms rounded open V with apex forward (pl. 116, fig. 11). Junction of rostral suture with facial suture not certainly recognized; may be exposed in specimen shown in pl. 116, fig. 11, in which anterior process is cemented in place.

Shallow wide lateral border furrows continuous from deep preglabellar furrow to genal angle. Similar posterior border furrows continuous with occipital furrow across deeper axial furrows or ending at axial furrows and thus separated from occipital furrow.

Thorax of Cutler specimen with 13 segments; thorax of lectotype disjointed, 12 segments visible. Thorax high with flanks of pleurae standing nearly vertically. Axial rings flat topped rather than "depressed" as described by Ulrich. Axial lobe slightly wider than pleural lobes and standing several millimeters above them in contrast to Ulrich's description in which axial lobe is said to be narrower than pleural. Pleurae flat topped, curving rather abruptly downward at fulcrum to a near vertical position. Inner parts of pleurae tend to slope slightly downward toward axial lobe and outer parts of pleurae spread, both conditions perhaps due to compression of specimens. Each pleura composed of an anterior and a posterior pleural band, posterior band continuous with axial ring of same segment. Pleural furrows present. Thorax narrows gradually posteriorly.

Pygidium sub-diamond shaped in outline, slightly wider than long, slightly shorter than glabella and occipital ring. Axial lobe distinct to within 4 mm. of posterior edge. Five axial rings and four pleural furrows distinguishable. Faint interpleural furrows present on inner part of pleural lobes but outer one-third of lobes lacking furrows of any kind. Posterior to fourth axial ring is semi-oval terminal lobe and behind this a curved axial ridge extends to posterior edge of pygidium. Pygidium of lectotype very poorly preserved.

Cephalon pygidium, and axial furrow areas of thorax tuberculate. Remaining surfaces probably tuberculate.

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JOURNAL OF PALEONTOLOGY, V. 34, NO. 5, P. 896–902, PLS. 117–118, 2 TEXT-FIGS., SEPTEMBER, 1960

STRUCTURE AND PRESERVATION OF *MASTOPORA PYRIFORMIS*, AN ORDOVICIAN DASYCLADACEAN ALGA

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ABSTRACT—*Mastopora pyriformis* (Bassler), long known in American literature as *Nidulites pyriformis*, is a mid-Ordovician dasycladacean alga. Thin-section study of specimens from the Chambersburg limestone of Virginia has revealed new details of the cortical skeleton, traces of the central vesicle, and gametocysts. The skeleton was composed of aragonite, and was dissolved after burial. The calcite spar which preserves the shape of the cortical skeleton is a later precipitate in the space which remained between the external mold and partial, displaced internal calcilutite fillings.

INTRODUCTION

FOR over 100 years, paleontologists have been concerned with centimeter-sized, bulb-shaped hollow calcareous bodies bearing hexagonal cups on their surface. These fossils, found in the Ordovician and Silurian rocks of the Baltic region, the British Isles, and the eastern United States, have been described under the generic names *Mastopora* Eichwald, *Nidulites* Salter, and *Cyclocrinus* Eichwald. They have been variously classified as *incertae sedis*, Foraminifera, sponges, corals, Bryozoa, and gastropod eggs, and are now known to represent dasycladacean algae. We have studied *Nidulites pyriformis* Bassler from the Chambersburg limestone of Virginia. This is definitely a member of the genus *Mastopora*. This study sheds new light on the structure of this species and of the genus, as well as on the peculiar conditions of preservation, and the depositional environment.

The specimens here used are part of the Princeton collections, and those illustrated are identified by number (see figure descriptions). They were collected in part by G. van Ingen, and in part by J. F. Mason, about 1 mile southwest of Strasburg, Virginia.

HISTORY OF STUDY

The history of the study of *Mastopora* and its relatives before 1896 has been related by Stolley (1896), and need only be touched on here. Klöden (1834) described and figured a *Mastopora* from glacial boulders in northern Germany, under the name of *Cellepora hexagonalis*. Eichwald (1840) erected the genus *Mastopora* (*M. concava*). He described an internal view of the skeletal wall from the Ordovician (Caradocian) of Estonia, but did not illustrate it. Salter (1851) erected the genus *Nidulites* (*N. favus*) for flattened molds from the lower Silurian (Llandovery) of Pembrokeshire. He tentatively interpreted this fossil as a "nest" or "clutch" of gastropod eggs, of the genus *Murchisonia*. In 1860 Eichwald emended his earlier description of *Mastopora* and provided illustrations. He placed this genus among the receptaculitids, and considered these as corals. Salter in 1865 placed *Nidulites* among the sponges. Kjerulf (1865) described *Nidalites* (sic) *favosus* from the Ordovician of Malmö Island (Sweden), and considered it to be a bryozoan. Bigsby (1868) placed *Nidulites* among the sponges and *Mastopora* among the Bryozoa. Nicholson and Etheridge (1880) added to the structural understanding of *Nidulites favus*, and called attention to the resemblance of *Nidulites* and *Cyclocrinus*, a close relative of *Mastopora*. In 1889 Nicholson and Lydekker suggested that *Nidulites* and *Cyclocrinus* might be dasycladacean algae ("siphonae verticillati").

Various succeeding workers concerned themselves with these forms, and allied them with various other fossil groups, but no real progress was accomplished until Stolley (1896) undertook a general revision of a group of these early Paleozoic problematica, including the genera *Mastopora* Eichwald, *Cyclocrinus* Eichwald, *Nidulites* Salter, and *Pasceolus* Billings. Stolley fully confirmed Nicholson's suggestions that these

fossils are the remains of dasycladacean algae. He clearly established the difference between *Cyclocrinus* and *Mastopora:* The former has calcified internal branches, and has calcareous lid-like covers over its cortical cells, whereas *Mastopora* lacks these skeletal elements.

The British *Nidulites favus* was found to differ from *Mastopora concava* Eichwald only in the shape of its cortical cells, presumably a character of no more than specific value. *Nidulites* Salter was therefore reduced to a junior synonym of *Mastopora* Eichwald.

Unaware of Stolley's work, Bassler (1909) figured a *Nidulites* sp. from the Ordovician Chambersburg limestone of Virginia. In 1915 he applied to it the new name *N. pyriformis*, and in 1919 he published a fuller description of this species. He considered it to be related to *Receptaculites* etc., and was undecided about assigning it either to the sponges or to the calcareous algae. Subsequent American authors (Butts 1940, Shimer and Shrock 1945, Cooper and Cooper 1946) followed his course, long after European workers (for example Pia 1926) had accepted Stolley's views, until Johnson (1954) listed the Virginia species as *Mastophora* (sic) *pyriformis* Bassler and assigned it to the Dasycladaceae. Johnson and Konishi (1959) reviewed the Silurian members of the genus.

STRUCTURE OF *MASTOPORA PYRIFORMIS* (BASSLER)

Our material contains three different kinds of structures belonging to *Mastopora:*

(1) External molds of the bulb-like cortical skeleton, underlain by coarsely crystalline calcite "casts" of the skeletal surface. These skeletal casts, the origin of which is discussed below, weather out readily, and previous knowledge of the species is based on them alone.

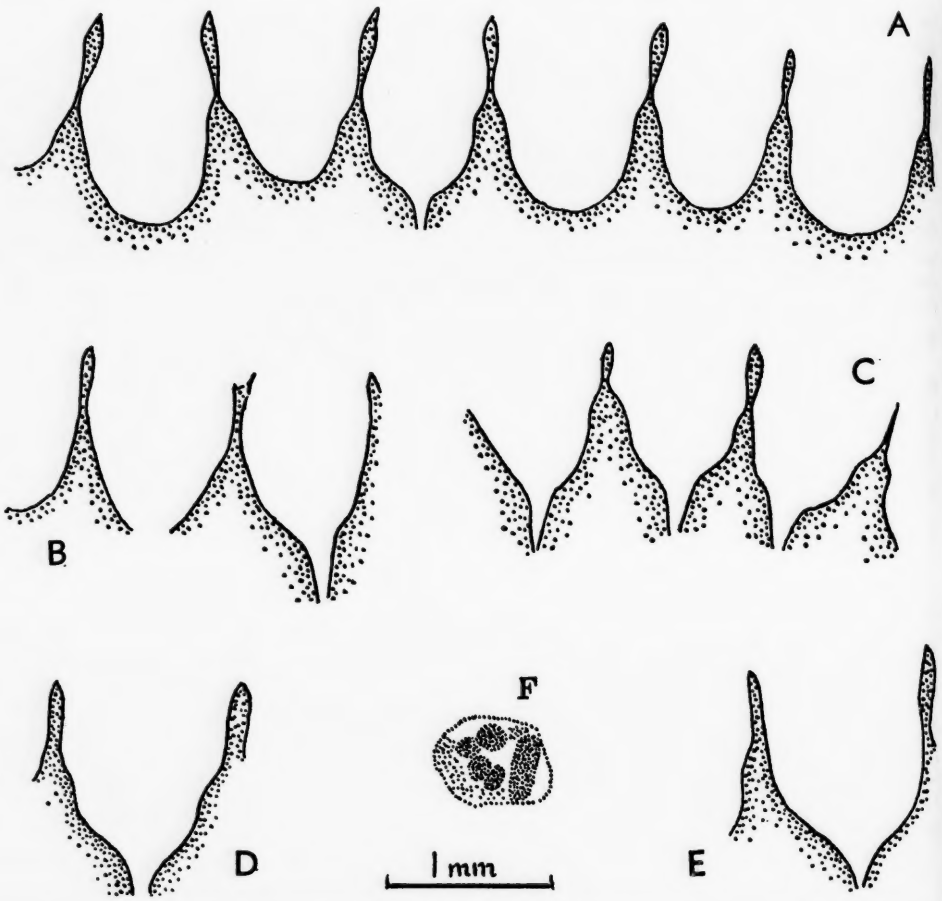
(2) Pyritized traces of the central vesicle in the center of the cortical bulb.

(3) Small, elongate pellets found in profusion, mainly in the interior of one specimen, and interpreted here as gametocysts of *Mastopora.*

Form of the cortical bulb. Bassler (1919, p. 193) described the general form of *Mastopora pyriformis* as follows: "The body is pyriform and pedunculate with an outer covering of hexagonal cuplike plates fused or articulated by their edges. On the exterior each plate is deeply concave and marked off at the surface by a sharp wall. The plates are smallest at the narrow end of the organism. The average diameter of the cups is one millimeter. The interior of the organism is hollow, frequently filled with crystalline calcite. Specimens are usually 35 mm. in length, sometimes 50 mm." The average width of our specimens is 14 mm.

The cell-cups. In accordance with the dasyclad affinities, to be discussed below, the concavities pitting the cortical skeleton are here termed cell-cups. The sharp rims dividing these cell-cups follow a hexagonal pattern, but below this rim, the cups are circular in outline, as may be seen in etched-out cell cups (plate 117, fig. 4) and in tangential sections (plate 117, fig. 2). In vertical sections the cups are seen to be goblet-shaped (text-fig. 1), and quite different in profile from the cups of the Baltic *M. concava*, figured by Stolley (1896). The cups average 1.2 mm. deep. Each cup bears in its base a tube-like continuation toward the interior, but in any given thin section only a few cups have been intersected precisely in the median plane, so as to show this structure (plate 118, fig. 3). Text-fig. 1 illustrates several examples. This "stem" of the "goblet" can be followed inward for only about 0.2 mm, and then is lost in the coarse calcite mosaic, a matter which will be explained below. The stems are passages through the original cortical skeleton, through which passed the delicate branches (comparable to the bristles of a bottle-brush) which connected the cortical cells with the central vesicle.

The central vesicle. Remnants of the central vesicle (also known as the trunk cell or central stem) may be seen in three of our specimens: A natural, weathered surface (plate 117, fig. 1), and two thin-sections (plate 117, figs. 3,5). It measures 2 mm. in diameter, and in the thin sections it appears to be outlined by organic matter and pyrite. It appears to have lacked any calcareous skeleton. Calcified central vesicles are known from many dasycladacean genera, but none has been reported to date for members of the genus *Mastopora.*



TEXT-FIG. *1A–E*, longitudinal sections of cortical cups; *F*, a group of gametocysts in sparry matrix, possibly representing a gametangium, *A,F*, 83733; *B*, 83735; *C*, 83732; *D,E*, 83737.

EXPLANATION OF PLATE 117

FIGS. *1–5*—*Mastopora pyriformis* (Bassler), from the Ordovician Chambersburg limestone of Virginia. *1*, Weathered specimen, ×5, showing cortical skeleton and central vesicle (V) (83740); *2*, Tangential thin-section of cortex, ×5, showing rounded outline of cortical cells (83739); *3*, Thin-section, ×5, showing cortical cups, remnant of central vesicle (V), and extensive filling by calcite spar (83741); *4*, External molds of cortical cups, ×11, prepared by etching a specimen in dilute acid: the sparry calcite etched faster than the calcilutite matrix, and left the cup-molds standing in relief (83755); *5*, Thin-section, ×5, showing longitudinal sections of cups on right, carbonaceous and pyritic remnant of central vesicle (V), partial mud filling which settled against external mold (lower right) after solution of skeleton, and extensive development of calcite spar filling remaining cavity (83737).

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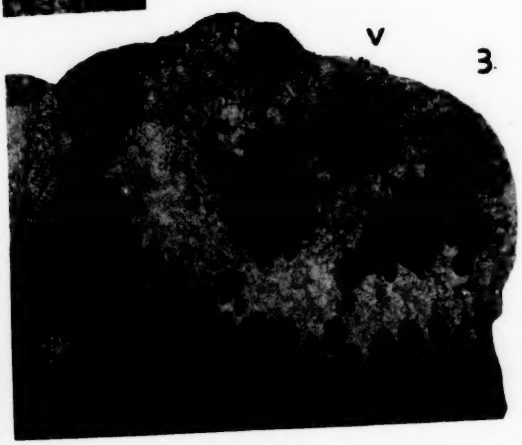
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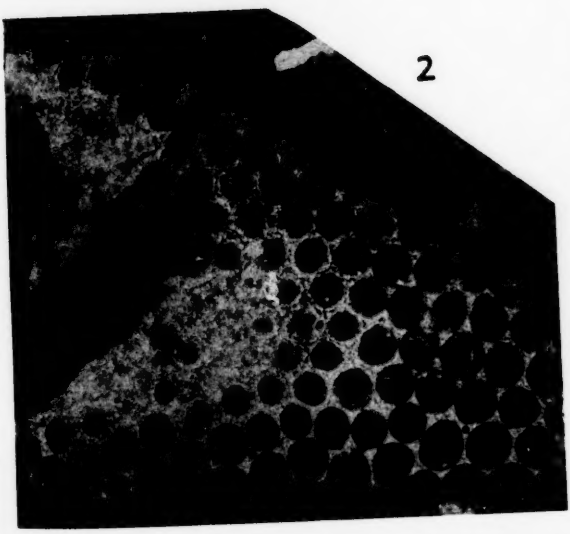
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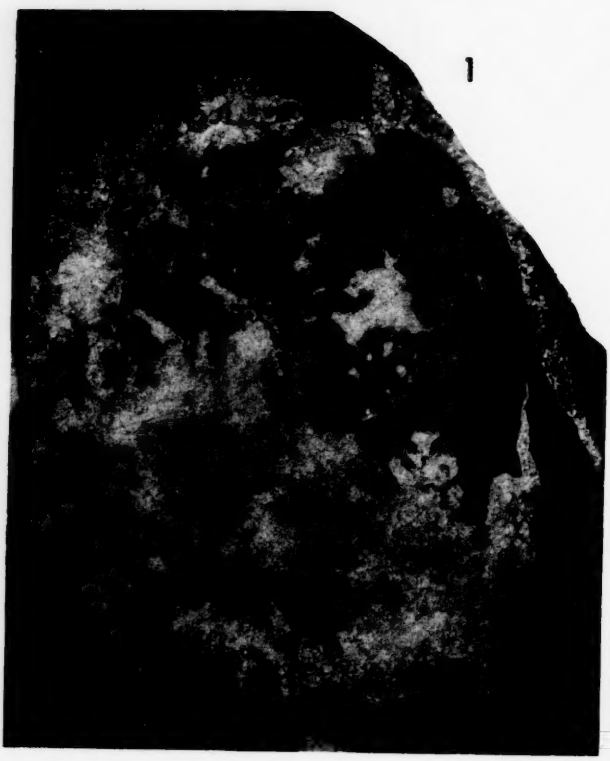

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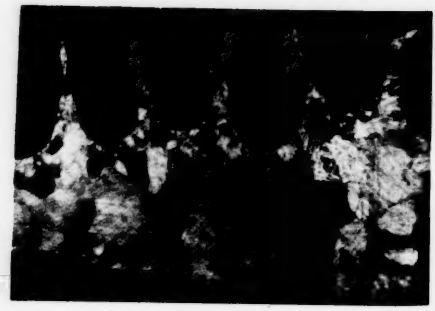

5

Gametal cysts. The reproduction of dasycladacean algae is carried on by gametes, which are housed in stout-walled round to ovoid capsules, the gametocysts. These gametocysts grow in special organs, the gametangia, which in primitive dasycladaceans were located in the trunk cell, and which in more advanced forms are found on the branches or in the cortical area.

The interior of one of our sectioned specimens (plate 118, figs. 1 and 2) is partly filled with ovoid bodies of fine-grained calcite, averaging 0.3 mm. long and 0.12 mm. wide, which we are inclined to interpret as gametocysts. Similar bodies, generally of clear calcite, are found scattered through the mud fillings and the matrix of other specimens. Of particular interest is a lens-shaped body of coarse calcite (adhering to the outside of one of the *Mastopora* skeletons) within which are to be seen traces of five of the inferred gametocysts (text-fig. 1F). This is interpreted as the remains of a complete gametangium.

CLASSIFICATION OF *MASTOPORA PYRIFORMIS*

The general structure of *Mastopora pyriformis* (Bassler) closely resembles that of the two other species referred to this genus. The species *M. pyriformis* is distinct from *M. fava* (Salter) in having deeper cell-cups, and from *M. concava* Eichwald in the profile of the cell cups as seen in longitudinal section. Its general pyriform shape is also distinctive.

As shown by Stolley, the genus *Mastopora* is closely allied to the genus *Cyclocrinus* Eichwald, which differs in showing calcification of the inner skeleton, and in having the cortical cells covered by variously ornamented calcareous lids. Pia (1926) placed *Mastopora* and *Cyclocrinus* into the tribe Cyclocrineae, one of 16 recognized tribes of the family Dasycladaceae Kuetzing (1843).

Among living algae, the genus *Bornetella* (a member of the tribe Neomereae) strikingly resembles *Mastopora* in general shape. It, also, has a pyriform shape and a cortex of closely packed cells.

This general similarity is probably more the result of convergence than of close relationship. The Cyclocrineae are known from the Ordovician, Silurian, Pennsylvanian and Permian. The Neomereae are known only from the Late Cretaceous onward. Those Cyclocrineae which have revealed the nature of their internal skeleton (such as *Cyclocrinus*) show simple branches, and it is therefore reasonable to assume that the branches of *Mastopora* were simple, whereas the Neomereae have compound branches. In *Bornetella*, for example, several cortical cells spring from a common branch, whereas the cell-cups of *Mastopora* show no similar convergence of their bases.

PETROGRAPHY AND MANNER OF PRESERVATION

Our samples of *Mastopora*-bearing Chambersburg limestone are fine-grained, conchoidally fracturing rocks (impure calcilu-

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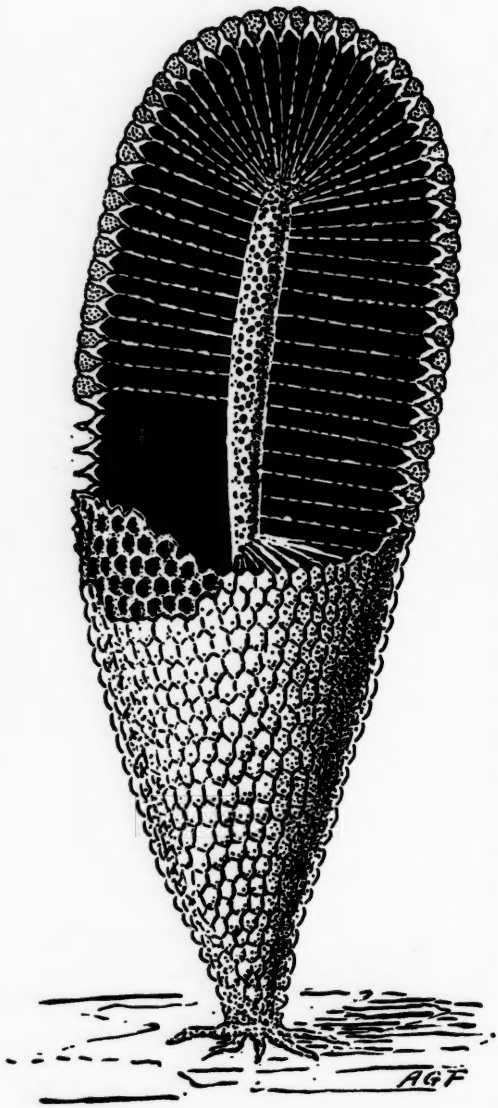
EXPLANATION OF PLATE 118

FIGS. *1–5*—*Mastopora pyriformis* (Bassler), from the Ordovician Chambersburg limestone of Virginia. *1*, Thin-section, ×5, showing interior filled with ragged patches of calcilutite, small ovoid bodies here interpreted as gametocysts of *Mastopora pyriformis*, and sparry calcite (83736); *2*, A portion of same, ×20, showing gametocysts; *3*, Thin-section, ×5, showing a series of six longitudinally cut cups (lower margin). Internal filling consists of partial filling of calcilutite, which settled toward right and fractured, and the succeeding filling by sparry calcite (83733); *4*, Transverse thin-section, ×5, of a specimen which was filled partly with silty calcilutite, partly with non-silty calcilutite, and which was rolled about on the bottom, picking up (in its cortical cups) first dark calcilutite, then a layer of silty calcilutite, then a layer of dark calcilutite, before becoming buried in slightly lighter calcilutite (83732); *5*, Portion of same, ×13, in cross-polarized light, showing that the sparry calcite developed as a cavity filling, after the skeleton itself had been leached away.



TEXT-FIG. 2—Diagrammatic reconstruction of *Mastopora pyriformis*. Soft parts shown are the *central vesicle* (also known as the "trunk cell" or "central stem"), the slender *branches* radiating out from it like the bristles of a bottle-brush, and their expanded tips—the *cortical cells* (stippled). Gametangia are not shown, because their position remains uncertain. The skeleton consists of the cortical cups, secreted by the cortical cells, and is shown without the soft parts in the mid-region of the left side.

tites) of graybrown to dark graybrown color. The most striking fossil is *Mastopora pyriformis*, but other fossil elements include the brachiopods *Christiania* and *Resserella* (with well preserved microstructure), well preserved to slightly silicified ostracodes, similarly preserved trilobites, similarly preserved bryzozoans, "recrystallized" microgastropods, numerous echinoderm ossicles of which some retain the original mesh-structure whereas others have lost it, and a variety of problematical spicules, etc. There are abundant pellets of mm. size, here interpreted as possible cell-casts of *Mastopora*, as well as smaller elongate pellets interpreted as gametocysts of the same genus.

The manner in which *Mastopora* is preserved differs markedly from that of the other fossils. No trace of the original skeletal material is to be found. The external surface of the original skeleton is faithfully preserved by the dark, fine-grained lime mud which was molded around it. Below this surface lies a mosaic of coarsely crystalline calcite retaining no remnants of original skeletal structures, and extending irregularly into the interior of the fossil. On the interior, this irregular envelope of calcite abuts sharply against the rounded outlines of an inner lime-mud filling. In some sections, this lime-mud core occupies an eccentric position: On one side it rests directly against the outer surface of the fossil (i.e. against the bases of the cell-cups) so that the crystal mosaic layer here is thin, interrupted, or lacking. On the opposite side, the crystal mosaic may extend into the center of the fossil.

The fabric and boundary relations of the crystal mosaic layer are significant to its interpretation. Almost everywhere the external and internal boundaries are smooth and rounded, and are not idiomorphically embayed by crystal grains of the mosaic. Also, the individual grains of the mosaic are nearly everywhere finest, and randomly oriented, at these boundaries. They grow coarser from either boundary toward the middle of the layer; and while no strikingly oriented fibrous or bladed fabrics have been developed, and in some areas the orientation of grains appears to be random in cursory

observation, the inner grains have elsewhere assumed columnar shapes (normal to the boundaries of the layer) and show parallel extinction (plate 188, fig. 5). It is therefore quite clear (Bathurst 1958) that the coarse crystal mosaic is the result of drusy cavity filling, not of recrystallization of skeletal material and/or lime mud filling. We must, therefore, assume that the original skeleton was dissolved away after burial, leaving a mold coextensive with such space in the interior as had not been filled with lime mud; and that this space was later filled by drusy crystal growth. The observation that the associated brachiopod, trilobite, ostracod, and echinoderm skeletons were not dissolved, and are preserved with their microstructure largely intact, indicates that the skeleton of *Mastopora* differed in composition; we infer that it was composed of aragonite. In centrally sectioned cortical cells the stalk may be followed inward into the crystal mosaic for about 0.2 mm.; this suggests that the skeleton was about 0.2 mm. thick.

The exterior matrix of the fossils also shows some peculiarities which shed light on depositional history: In one of the sectioned specimens (plate 118, fig. 4) the filling of the cell cups is distinct from the surrounding matrix: most of it is darker and more fine-grained, but all along one side of the specimen the cups contain a lamina of quartz and calcite silt particles. It would seem that this specimen rolled about in several kinds of sediment, which adhered to it within the cups, until it reached its final burial place.

GENERAL SUMMARY

Mastopora is thus seen to be a dasycladacean alga, of the general form of the Recent (probably convergently evolved) *Bornetella*. Remnants of the central vesicle are preserved as films of organic matter and pyrite. The branches have not been preserved except for their distal ends. They are believed to have been simple. The outline of the cortical cells has been preserved due to the secretion of calcareous cortical cups, which form a skeletal cortical bulb. The cortical cells of *M. pyriformis* (Bassler) differ from those of *M. favosa* from the Silurian of northwestern Europe, and from those of *M. concava* from the Caradocian of the Baltic region. The overall shape of *M. pyriformis* is also distinctive.

The cortical bulb skeleton of *Mastopora* was composed of aragonite. We assume that the algae lived on shallow, sunlit bottoms, either rooted on scattered shells or on local patches of calcarenite, from which they became distributed into the muddy areas after death. The bulbs were rolled about on the sea floor, and became partly to largely filled with calcareous mud before burial. After burial the external matrix became more or less firmly consolidated, while the interior mud fillings remained soft. Then the aragonite skeleton was leached away. Each fossil now consisted of (1) an external mold, (2) an inner lime-mud core, and (3) a cavity, resulting from (a) primary pore space within the skeletal bulb, and (b) the space created by solution of this skeleton. The inner lime-mud core lodged in the bottom of this cavity, resting on the cup-fillings of the external mold. At this time, when the external matrix was hard enough to maintain the shape of the cup-fillings, the internal lime-mud core was evidently still quite soft; its surface does not seem to retain any mold-impress of the internal surface of the skeleton; instead, various sections (for example plate 117, fig. 5 and plate 118, fig. 3) show that it became molded around the projections (cup-fillings) of the external mold. Oddly enough, the upper surface of this mud-core does not appear to have been level as is usual in such partial cavity fillings. Instead, the upper surface appears hummocky, and in some sections the core appears to have shrunk and to have cracked (plate 118, fig. 3), as though the sediment has emerged from the sea and had dried out at this critical time, or as though some similar dehydrating process had gone on under water.

Finally, the cavity became filled by drusy growth of calcite, extending inward from all walls.

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ACROTHORACIC BARNACLES FROM THE TEXAS PERMIAN AND CRETACEOUS

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ABSTRACT—*Rogerella cragini*, n. sp., a burrow of a heretofore undescribed species of acrothoracic barnacle, is restricted to host shells of *Ceritella proctori* (Cargin), a gastropod. *R. cragini* is known only from the Edwards limestone (Middle Albian) of Travis County, Texas.

A second, indeterminate, acrothoracic barnacle burrow occurs on silicified shells from the Word formation of the Glass Mountains, Texas.

INTRODUCTION

FOSSIL Acrothoracica have not previously been described from the Americas. Young (1952) inadvertently illustrated burrows of these barnacles and Saint-Seine (1954) recognized their true nature from the illustrations of the burrowed gastropods.

The Acrothoracica constitute a small group of specialized Cirripedia which burrow into the shells of other animals. They are not known to be parasitic. Most species never penetrate through the shell, but if the host is thin-shelled penetration may occur (Codez and Saint-Seine, 1958), to which the host reacts by precipitating new shell material much as pelecypods react to penetration by such borers as *Cliona*. The adult barnacle lives in the burrow with appendages retracted except for feeding (Tomlinson, 1955).

Fossil Acrothoracica have recently been reviewed by Codez and Saint-Seine (1958). They point out that the fossils of this order were first recognized and described by Zapfe (1936). Further, they add that definite Acrothoracic burrows are known from the Permian, Jurassic, Cretaceous, Tertiary, and Recent, with more doubtful representatives known from the Upper Devonian, Carboniferous, and Triassic.

Of the two species described below, one is Cretaceous and the other Permian.

SYSTEMATIC PALEONTOLOGY

Phylum ARTHROPODA
Class CRUSTACEA
Subclass CIRRIPEDIA
Order ACROTHORACICA
Family ROGERELLIDAE Codez and Saint-Seine, 1958

Genus ROGERELLA Saint-Seine, 1951

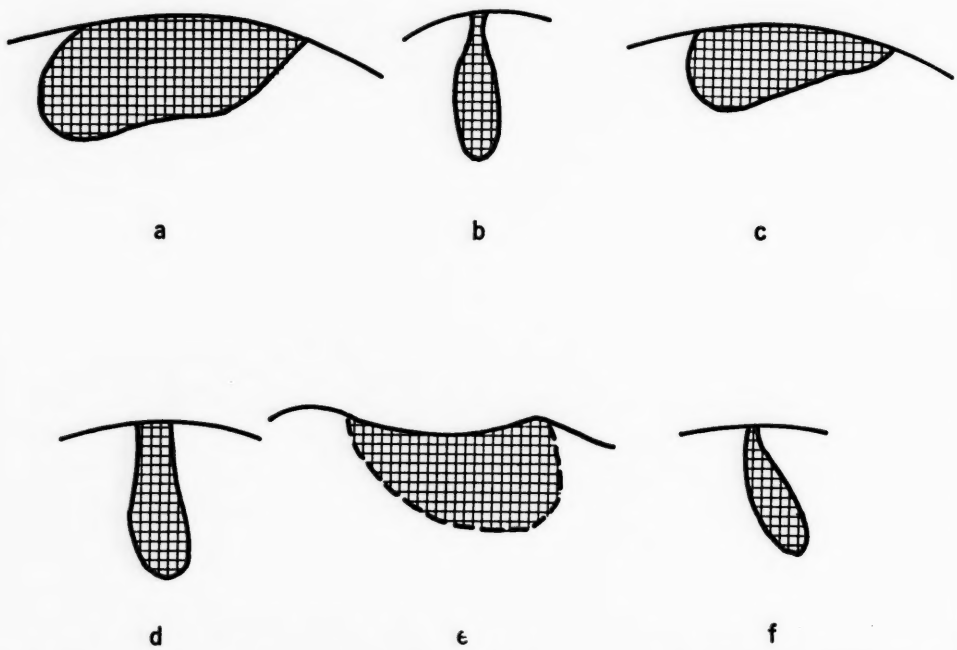
ROGERELLA CRAGINI, n. sp.
Pl. 119, figs. 1–15; text-figs. 1a–d,f,2.

Holotype.—The specimen on the left in figure 14, pl. 119, from UT 33050, Edwards limestone, Deep Eddy Bluff, Colorado River, Austin, Travis County, Texas.

Specific characters.—Aperture of burrow comparatively short for acrothoracic burrows, wide, subelliptical, virgulate, sometimes hooked to the right, more often hooked to the left as viewed. The apertures range from 0.8 to 1.9 mm. in length, and from 0.3 to 0.7 mm. in width. The burrow is clearly divided into two parts, an anterior peduncular slot or groove, and a posterior, widening opening; the two parts join at an angle which varies according to the location of the burrow on the shell of the host. A bourrelet is rarely present, but traces of one can be seen on some individuals (pl. 119, fig. 5). Most burrows show original attachment at the suture line of the gastropod host.

The median longitudinal section shows the burrow to be slightly less than $\frac{1}{2}$ as deep as it is long, the floor of the burrow gently inclined from anterior to posterior, with the posterior end of the section rounded. The transverse section shows narrowing of the aperture, particularly toward the anterior end. There is no consistent lateral inclination.

Observations.—*Rogerella cragini*, n. sp., is not quite as large as *Rogerella mathieui* Saint-Seine (1955), the maximum length of the latter being 2.0 mm. and width 0.8 mm. The maximum length of the American species is 1.9 mm. and the width 0.7 mm. The proper significance of these figures can be

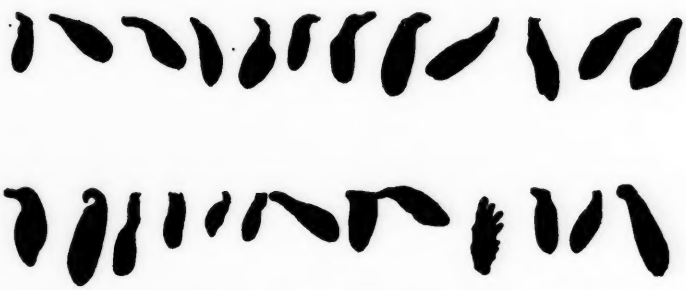


TEXT-FIG. *1—a–d,f—Rogerella cragini*, n. sp.; *a*, longitudinal section from UT 33047 (*see also* Pl. 119 fig. 4); *b,d*, transverse section from UT 33048 (*see also* pl. 119; figs. 5,6,10); *c,f*, longitudinal and transverse sections from UT 33052; *All*, ×14.5.
e—Acrothoracic barnacle burrow genus and species indeterminate; (*see also* pl. 120, figs. 4,7); ×14.5.

calculated, but not interpreted, because there is no way of determining whether a small adult or a large juvenile is being measured at any certain size. The bourrelet seems to be just as rare in the European species (Saint-Seine, 1955) as in the American. The hosts of *R. cragini* are preserved as hematitic calcite casts; most of the fossils have suffered some corrosion of morphologic detail, and, until contradictory evidence is obtained, we are assuming that the burrow apertures and bourrelets have suffered corrosion, because some burrows (pl. 119, fig. 5) show a small remnant of a bourrelet. One burrow (pl. 119, fig. 6) may have had a double bourrelet, as does the holotype of *R. mathieui* (Saint-Seine, 1955). The bourrelets of the European species are described as very fragile, thin, and usually absent, the double bourrelet being extremely rare (Saint-Seine, 1955).

The greatest difference between *R. mathieui* Saint-Seine and *R. cragini*, n. sp., is the shallower wedge-shaped burrow of the latter, with the point of the wedge anterior; *R. mathieui* has a deep, rounded burrow in median longitudinal section.

Rogerella cragini, n. sp., is known only from the Edwards limestone, and from along the Colorado River, Travis County. Shells from similar reef masses in Williamson County do not have any barnacle burrows. The hosts are shells of *Ceritella proctori* (Cragin) in a thanatocoenose. The shells of the host have been concentrated in little piles along bedding planes. Apparently they were gathered together in pockets of lower energy water after death of the animal. There is no indication of burrows in hosts while the host was still alive as in Recent *Trypetesa* (Tomlinson, 1955), as the burrows are restricted to the upper side of the shell after the shell was deposited. A few shells have been rolled over, or partly over,



TEXT-FIG. 2—Outlines of apertures of burrows of *Rogerella cragini*, n. sp., from the Edwards limestone. Those burrows with the peduncular slots at the suture of the host have been selected for these outline drawings, illustrating variation in form and geniculation; all, ×2.7.

and have received a new cycle of barnacle burrows, but even the disturbing of shells after their first deposition seems to have been unusual.

Although there are many other gastropods in the fauna, including other species of *Ceritella*, such as *Ceritella glabra* (Stanton), only shells of *C. proctori* serve as hosts of *R. cragini*. Examination of many individuals of *Toucasia patagiata* (White), *Monopleura marcida* White, *M. pinguiscula* White, *Lucina acutelineata* (Römer), *Caprinuloidea crassifibra* (Römer), *Cladophyllia furcifera* Römer, and all of the many species of gastropods revealed not a single burrow of *Rogerella cragini* on any host shell other than *Ceritella proctori*. The associated fauna of the Edwards limestone is that listed by Young (1952). The high specificity to the host shell is not understood since burrowing was after death of the host animal. Possibly the barnacle colonies are rare, and this single thanatocoenose had optimum survival conditions to barnacles, and that other sediments representing like optimum survival conditions have not been collected. It is also quite apparent that the *cypris* larva needed protection when it started to attach. Saint-Seine (1955) points out that the *R. mathieui* larva often sheltered in an ambulacral pore or a tubercle perforation for attachment. The individuals of *R. cragini* obviously sheltered in the spiral sutures of the gastropods, since about 90% of the peduncular slots originate at sutures.

Another aspect of the American species, *Rogerella cragini*, n. sp., differing from the European, *R. mathieui* Saint-Seine, is in its biotope. European forms of *Rogerella mathieui* are restricted to echinoid hosts in the Jurassic and Cretaceous, but are known from hosts of other groups after the Cretaceous (Codez and Saint-Seine, 1958). Saint-Seine (1955) points out that as long as no morphologic comparison is possible, distinction on the basis of biotope is doubtless legitimate, since most acrothoracics have a high host specificity, but that such distinction serves no useful purpose.

Species and genera of living acrothoracics are designated entirely on soft parts. The taxonomy and nomenclature of fossils are based on burrows, and form taxa result.

Horizon and locality.—All specimens (probably 40 or 50 host shells) of *Rogerella cragini*, n. sp., are from the Edwards limestone, about 75 feet from the top, Deep Eddy Bluff and Red Bud Trail, Colorado River, Austin, Travis County, Texas; upper part of the Middle Albian.

Order ACROTHORACICA ?
Family Indet.
Genus Indet.
Species Indet.
Pl. 120, figs. 1–14; text-figs. 1e,3.

Observations.—A number of small Permian fossils from the Glass Mountains of

TEXT-FIG. 3—Outline drawing of apertures of acrothoracic burrows, genus and species indeterminate, from the Word limestone of Trans-Pecos Texas; ×5.4.

Trans-Pecos Texas have been burrowed by what appears to have been acrothoracic barnacles. Occurring on several species of brachiopods (pl. 120, figs. 4,6,7,11–13) their apertures are elliptical, straight, with slight angulations at loci of greatest curvature. The widths of these burrows range from 0.3 to 0.5 mm., and their lengths from 0.6 to 1.0 mm. The burrows, if they can be called that, completely penetrate the shell. Penetration may result from (1) parasitism, in which the occupants of these burrows could not be referred to the Acrothoracica, (2) poor preservation with the inner layer of shell material not being replaced during silicification, thus destroying the inner wall of the burrow, or (3) poor preservation resulting in the inner wall of the burrow being so fragile that it was destroyed during acidization.

The longitudinal section (text-fig. 1e) is interpretive because the details of structure were destroyed during silicification. The best interpretation is that the burrow penetrated the shell, and the host reacted by depositing a layer of shell material over the burrower, as pelecypods react to *Cliona*.

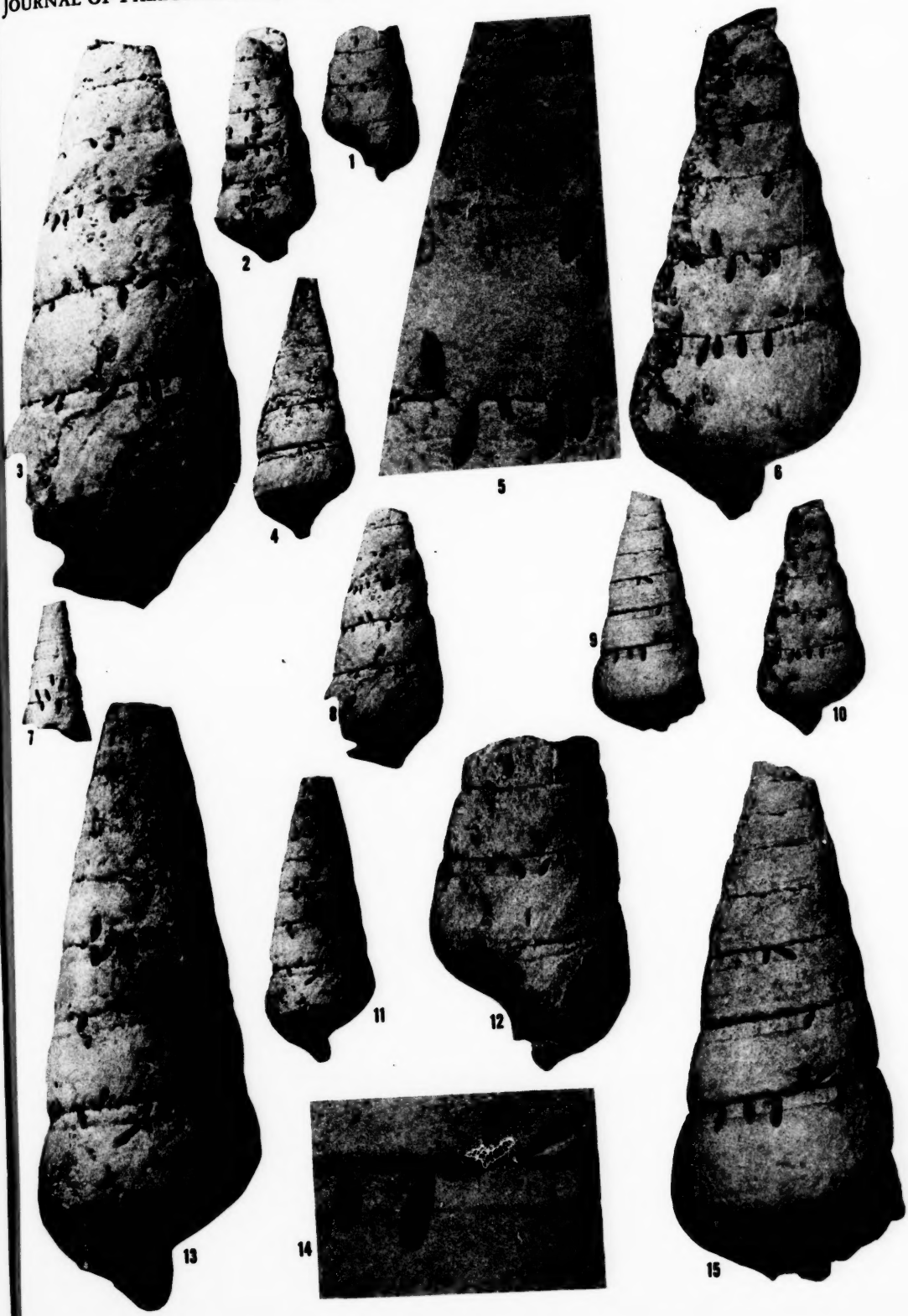
The elongate holes in the several species of Bryozoa (pl. 120) appear to belong to the same group of animals that burrowed the brachiopods, but the margins of the burrows in the Bryozoa are broken up where they intersect the zooecia until the burrow shape cannot be determined.

Horizon and locality.—Word formation

(*Text concluded on next page.*)

EXPLANATION OF PLATE 119

FIGS. *1–15—Rogerella cragini*, n. sp., on host shells of *Ceritella protcori* (Cragin); *1,12*, UT 33044; *2*, UT 33045; *3,8*, UT 33046; *4*, UT 33047 (*see also* text fig. 1a); *5,6,10*, UT 33048 (*see also* text-figs. 1b and 1d); *7*, UT 33049; *9,14,15*, holotype, UT 33050 (the holotype is the left individual on figure 14); *11,13*, UT 33051; *1,2,4,7–11*, ×1; *3,6,12,13,15* ×2; *5,6*, ×5.4. All from Deep Eddy Bluff, Colorado River, Austin, Travis County, Texas.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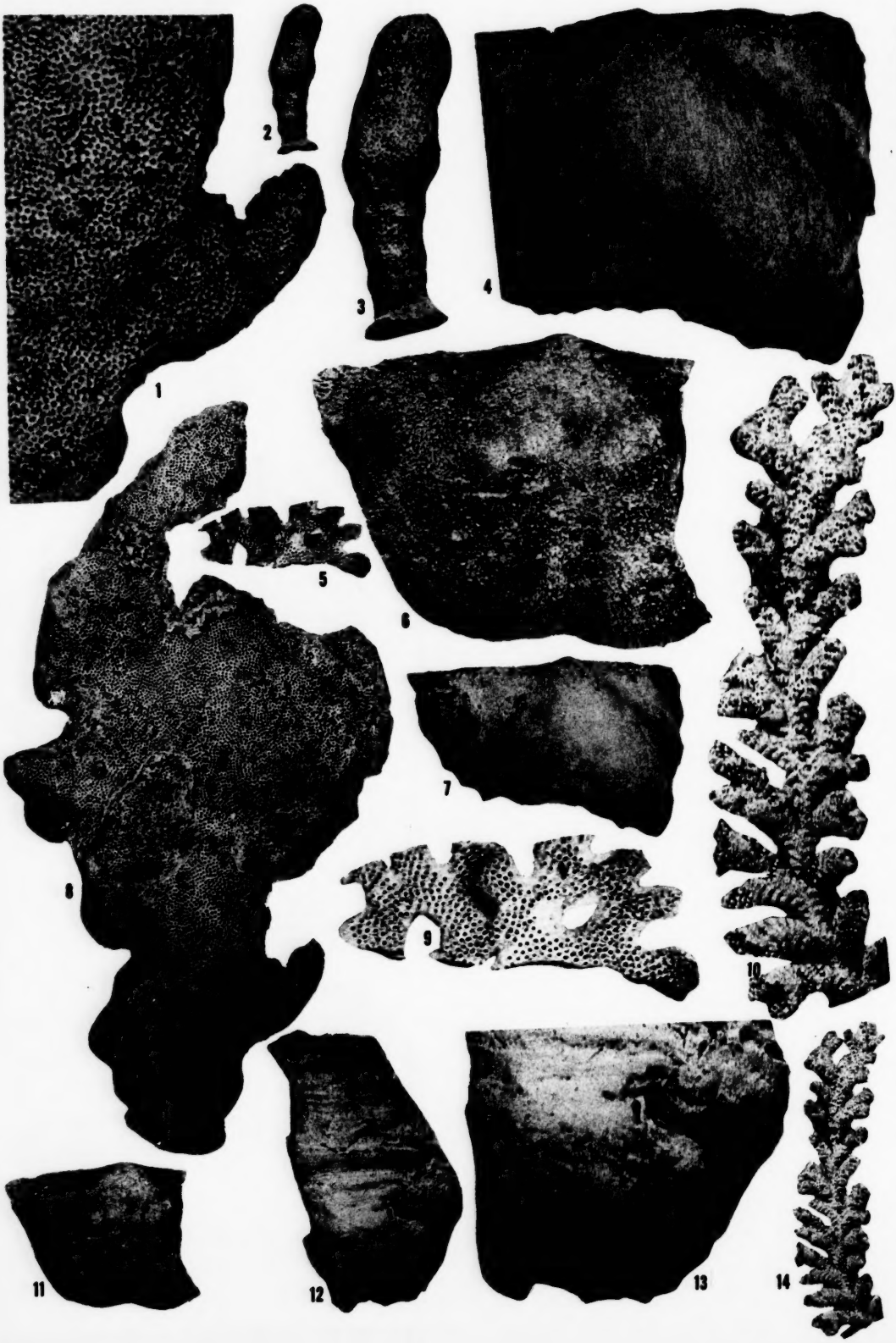
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(top of limestone no. 3), from the east side of a small arroyo, 4.1 miles N. 34° E. of the Hess ranch house, Hess Canyon Quadrangle, Texas (locality 706e).

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MANUSCRIPT RECEIVED AUGUST 22, 1959.

EXPLANATION OF PLATE 120

FIGS. *1–14*—Acrothoracic barnacle burrows, genus and species indeterminate, on hosts of various brachiopods and bryozoans; *2,5,7,8,11,14*, ×1; *1,3,4,6,9,10,13*, ×2; *2,3*, UT 30570; *1, 4–14*, UT 33053; all from the Word formation, Glass Mountains, Texas.

JOURNAL OF PALEONTOLOGY, V. 34, NO. 5, P. 908–922, PL. 121, 8 TEXT-FIGS., SEPTEMBER, 1960

MARINE AND FRESH WATER FOSSILIFEROUS BEDS IN THE POTTSVILLE AND ALLEGHENY GROUPS OF WESTERN PENNSYLVANIA[1]

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ABSTRACT—Stratigraphic and paleontologic studies of the Pottsville and Allegheny groups of western Pennsylvania have resulted in the establishment of twelve, environmental, faunal zones some of which have proved useful in regional correlation and paleogeographic interpretations.

Marine and restricted marine fossils, mainly *Chonetes*, *Mesolobus*, *Marginifera*, *Lingula*, *Dunbarella* and *Aviculopecten* occur in dark-gray shales above the Upper Mercer, Lower Clarion, Upper Clarion, Scrubgrass, Lower and Middle Kittanning coals. Fresh water fossils, mainly estherids and *Carbonicola* are found in shales above the Upper Kittanning, and Lower and Upper Freeport coals, and ostracods and small gastropods are found in the limestones below these coals.

The most rapid faunal variation in all marine beds takes place in a general north-south direction. The marine fossils disappear to the north and east in the Upper Mercer and Lower Clarion shales, whereas they disappear to the northwest and southeast in the other beds.

INTRODUCTION

THE purposes of this paper are to describe the character and distribution of invertebrate fossils in the Pottsville and Allegheny Groups of western Pennsylvania and to show how these fossils have been applied to correlation and paleogeographic problems. The investigation was conducted intermittently during the past six years and involved the collection and identification of invertebrate fossils from approximately 200 measured sections. No exhaustive speciation was attempted and not all fossiliferous beds were sampled in detail. The main effort was placed on shale beds in which fossils have not previously been reported or described.

The area investigated lies within the Allegheny Plateau region of western Pennsylvania. Structurally it occupies the northeastern part of the Pittsburgh-Huntington synclinorium as shown in text-fig. 1. Most of the sampling was confined to the east-west trending outcrop belts.

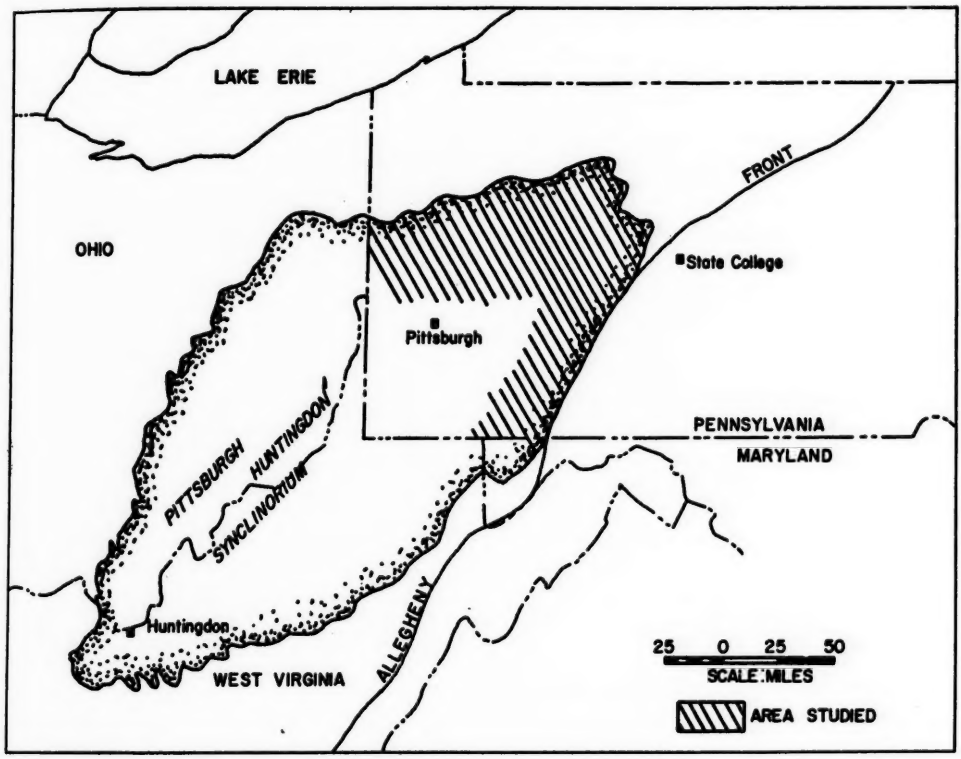
ACKNOWLEDGMENTS

The initial part of this work pretaining to Clearfield County was part of a Ph.D. dissertation submitted to the Department of Geology of The Pennsylvania State University. Dr. F. M. Swartz supervised this thesis. The remainder of the work and preparation of the manuscript was done in the Mineral Conservation Section of The Pennsylvania State University under the direction of Dr. M. L. Keith. Dr. Keith critically read the manuscript. The diagrams were drafted by R. B. Weiss.

PREVIOUS WORK

The invertebrate fauna of the Pottsville and Allegheny groups in Pennsylvania have received relatively little attention from stratigraphers. Raymond (1910) described the fossils of the Vanport limestone from several sections in western Pennsylvania. Davis (1930) studied fresh-water mollusca of the genus *Carbonicola*, *Anthracomya* and *Niadites* from the anthracite coal fields of Pennsylvania and the bituminous fields of western Pennsylvania, Virginia, and Kentucky. Ferm (1957) listed about 35 marine species from the Kittanning formation in parts of Jefferson County, Pennsylvania and discussed their environmental significance. Williams (1957) described about 30 species from the Allegheny rocks in Clearfield County and discussed their use in correlation and environmental interpretations. The study of Allegheny fauna in adjacent states has also been sporadic. Stout (1931) recognized five marine fossil zones in the lower Allegheny of eastern Ohio. The *Nautiloidea* of these zones has been described by Sturgeon (1946). Price (1921) described and dis-

[1] Contribution No. 59-27, Mineral Conservation Series from the College of Mineral Industries, Pennsylvania State University.



TEXT-FIG. *1*—Index map.

cussed the occurrence of marine fossils in the lower Allegheny rocks of West Virginia.

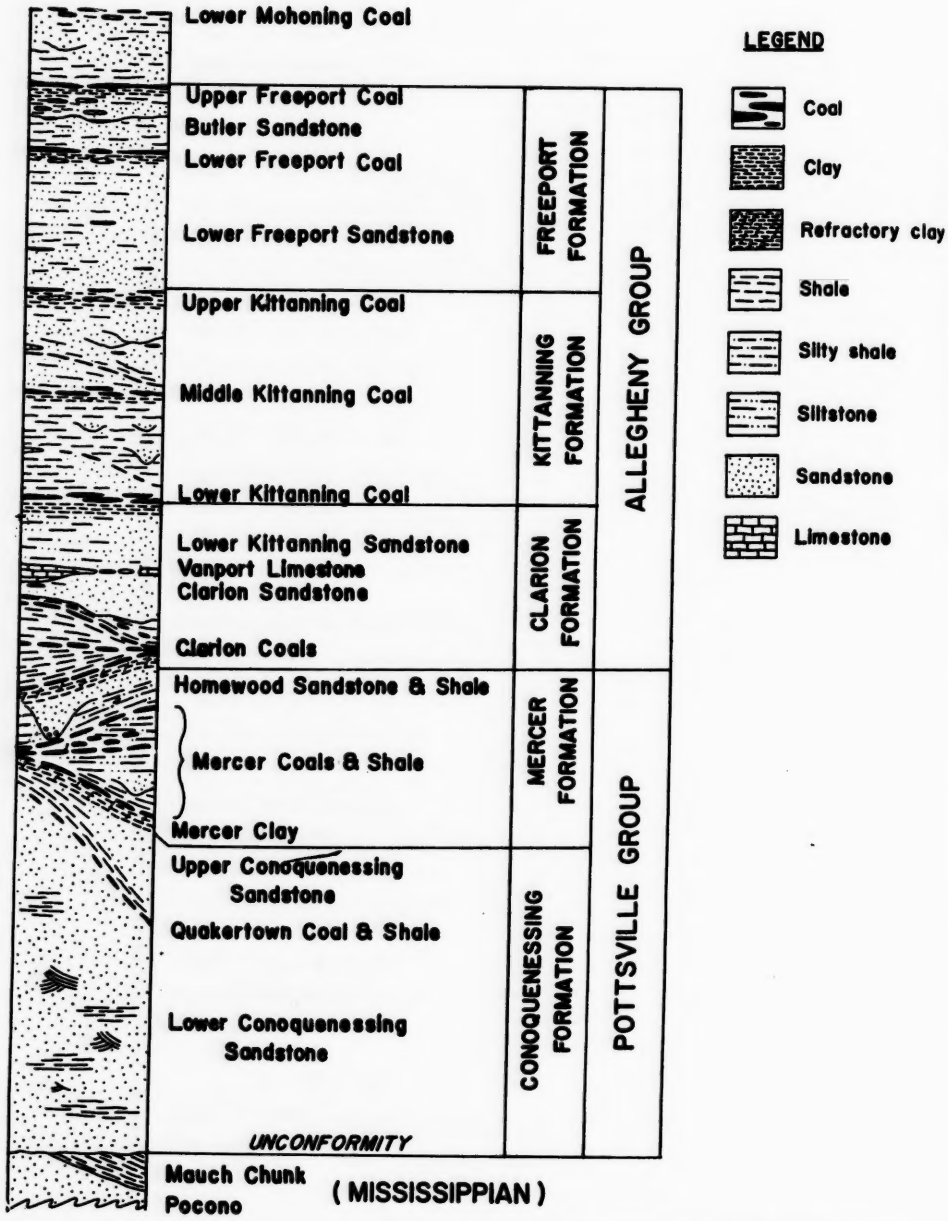
In contrast to the rather casual study of the Allegheny fauna of the Appalachian coal basin, extensive and detailed work has been done on fauna from the underlying Pottsville series and the overlying Conemaugh series. Morningstar (1922) described an abundant fauna, largely marine, from the Pottsville of Ohio. Mark (1912) studied the marine fossil zones of the Conemaugh in Ohio. Price (1914) published extensively on the fauna of the Pottsville and Conemaugh series of West Virginia. C. K. Swartz (1920) recorded the marine fossil zones in the Pottsville and Conemaugh of Maryland, and illustrated relationships to the marine zones in western Pennsylvania, Ohio and West Virginia.

GENERAL STRATIGRAPHY

An idealized stratigraphic section of the Pottsville and Allegheny Groups in western Pennsylvania is shown in text-fig. 2. Data used in construction of the diagram were compiled from the work of Ashley (1940), Graeber & Foose (1942), Ferm (1957), De Wolfe (1929), Williams & Nickelsen (1958), Williams (1957) and unpublished work of the writer.

The Pottsville and Allegheny constitute the lower two groups of the Pennsylvanian in western Pennsylvania. The Pottsville, unconformably overlying the Mississippian, averages about 240 feet in thickness. Throughout most of western Pennsylvania, the lower two-thirds of the Pottsville consists of massive sandstone (the Connoquenessing formation), and the upper one-third of a highly variable sequence of clays, coals, shales and sandstones (the Mercer formation). In extreme western Pennsylvania, the Sharon conglomerate forms the basal Pottsville but that unit was not observed in any sections in the area studied.

The Allegheny Group, overlying the Pottsville, averages 280 feet in thickness. It



TEXT-FIG. 2—Generalized section of Pottsville and Allegheny groups in western Pennsylvania.

consists of six major coal zones between which occur variable sequences of shale, limestone, sandstone, clay and thin coals. The major coal zones and their associated underclays are the most persistent beds whereas the sandstones are lenticular and irregular in occurrence. The Allegheny group has been arbitrarily divided into three formations at certain economically important or widely recognizable coal beds. These are, from bottom to top, the Clarion, Kittanning and Freeport.

NATURE AND OCCURRENCE OF FOSSILS

The invertebrate fossils of the Pottsville and Allegheny rocks occur mostly in shales, silty shales and limestones, varying in thickness from several inches to 20 feet. Considering all fossiliferous beds throughout the area, fossils are not very common, although locally abundant. Limestones (fresh-water), occurring in underclays beneath coal beds are fossiliferous, but invertebrate fossils are rarely found in the sandstones, underclays or coals.

Fifty-three genera, of which 36 have been identified as to species, were recognized in the present study. The most frequently occurring genera are relatively few in number, *Lingula*, *Chonetes*, *Mesolobus*, *Marginifera*, *Dunbarella*, *Aviculopecten*, *Anthraconauta* and *Estheria* constituting over 90 percent of the observed assemblage.

Table 1 shows the distribution of genera and species in the Pottsville and Allegheny groups. Of the 53 genera identified, only 7 occur stratigraphically above the Upper Kittanning coal and these are mainly conchostrachans. In rocks stratigraphically below the Upper Kittanning coal, the majority of genera are confined to shales and limestones above the Upper Mercer, Lower Clarion, Upper Clarion, Scrubgrass, Lower Kittanning and Middle Kittanning coals. Brachiopods constitute the majority of genera present in these beds.

In view of the restriction of invertebrate fossils to thin beds within the respective lithologic members and the changes in general character of fossil assemblages from member to member, it is reasonable to conclude that the faunal variations are mainly the result of environmental changes. Some of the fossil assemblages are recurrent; for example, many of the lower and middle Allegheny brachiopods appear again in Conemaugh sediments, higher in the section.

ENVIRONMENTAL CLASSIFICATION OF FOSSILS

In order to evaluate faunal variability within and between the various fossiliferous beds, it was found convenient to classify the fossils into several, inferred environmental groups. These groups together with associated rock types are shown in table 2. The classification is based upon faunal associations observed in the present study and those described in the literature. Characteristic fossils of each group are shown in plate 121.

The marine character of the fossils listed in groups 1, 2 and 3, with one exception, are fairly well established (Weller, 1956, 1957; Trueman, 1954; Wanless, 1939; Elias, 1937). The exception is *Anthraconauta* (and lamellibranchs in general) which Trueman (1954) and most European geologists believe to indicate fresh water environments, whereas Weller (1956) believes them to have been inhabitants of brackish or marine water.

The conchostrachans *Estheria* and *Leaia* are not found associated with any of the marine or restricted marine fossils in the rocks studied and are believed to be of fresh-water origin. Weller (1957) regards *Leaia* as a fresh-water fossil and *Estheria* as brackish.

Other independent evidence which supports the broad classification of Pennsylvanian sediments into marine and fresh-water groups on the basis of fossils is provided by the geochemical studies of Degens, *et al.* (1957, 1958). These investigators, analysing certain common and trace elements in shales and limestones, grouped by the faunal criteria presented in table 1, were able to differentiate the fresh water shales and limestones from the restricted marine and marine ones but were unable to distinguish any of the three marine groups from each other. Comparisons of the diagnostic elements, with their distribution in modern sediments and environments, led these workers to conclude that the inferred fresh-water or marine character of the Pennsylvanian rocks studied was determinable by trace element assemblage as well as by fossil assemblage.

REGIONAL CORRELATION

Text-fig. 3 shows the thickness, stratigraphic position and regional correlation of all major coals and fossiliferous beds in the Pottsville and Allegheny groups of western Pennsylvania. Each section shown in text-fig. 3 and located on the map (inset, text-fig. 3) is a composite of approximately ten closely spaced sections which average about 100 feet in thickness. The composite sections are not necessarily representative of the counties in which they occur.

Section 5 is located in the Allegheny

TABLE 1—DISTRIBUTION OF GENERA AND SPECIES IN THE POTTSVILLE AND ALLEGHANY GROUPS

	Upper Mercer Shale and Limestone	Lower Clarion Shale	Upper Clarion Shale and Limestone	Vanport Limestone	Lower Kittanning Shale and Limestone	Middle Kittanning Shale	Johnstown Limestone	Upper Kittanning Shale	Lower Freeport Limestone	Lower Freeport Shale	Upper Freeport Limestone	Upper Freeport Shale
COELENTERATA												
Lophophyllum profundum (Milne-Edwards & Haime)	x		x	x		x						
BRYOZOA												
Fenestella sp.	x		x	x	x							
ECHINODERMATA												
Crinoid stems	x		x	x		x						
BRACHIOPODS												
Lingula carbonaria Shumard	x	x			x	x						
Orbiculoidea missouriensis (Shumard)	x	x	x		x	x						
Wellerella sp.			x									
Derbya crassa (Meek & Hayden)	x		x	x	x	x						
Chonetes granulifer Owen			x		x							
Mesolobus mesolobus var lioderma Dunbar & Condra			x	x	x	x						
Mesolobus mesolobus var decipiens (Girty)	x		x	x	x	x						
Lissochonetes sp.	x											
Juresania sp.	x				x							
Linoproductus prattenianus (Norwood & Pratten)	x				x	x						
Dictyoclostus americanus Dunbar & Condra			x	x	x							
Marginifera muricatina Dunbar & Condra	x		x		x	x						
Marginifera wabashensis Norwood & Pratten	x											
Punctospirifer kentuckyensis (Shumard)			x	x		x						
Spirifer opimus Hall	x		x	x								
Squamularia perplexa (McChesney)	x		x	x								
Composita subtilata (Hall)	x		x		x	x						
Composita argentea (Shepard)				x								
Composita ovata Mather					x	x						
Amboceolia planoconvexa (Shumard)			x			x						
PELECYPODA												
Lima retifera Shumard	x				x							
Anthraconaia sp.					x							
Anthraconauta phillipsi (Williamson)	x	x	x		x							
Anthraconauta minima (Ludwig)					x							
Myalina aff. cuneiformis Gurley					x							
Myalina sp.	x		x		x							
Leda bellistriata Stevens			x									
Allerisma terminale Hall	x				x	x						
Aviculopecten eaglensis (Price)	x				x							
Aviculopecten occidentalis (Shumard)					x							
Dunbarella whitei (Meek)		x	x		x	x						
Stroblochondria sculptilis (Miller)					x							
Nucula sp.	x		x			x						
GASTROPODA												
Pleurotomaria sp.						x						
Dawsonella meeki (Bradley)				x	x							
Worthenia tabulata Conrad					x	x						
Euphemites carbonarius (Cox)	x				x							
Schizostomata catilloides (Conrad)			x		x							
Meekospira sp.					x	x						
Sphaerodoma brevis White	x				x							
Aclisima robusta Stevens					x							
Gastropoda undetermined	x		x			x	x		x		x	
CEPHALOPODA												
Pseudorthoceras sp.	x		x		x	x						
Metacoceras sp.			x		x							
ARTHROPODA												
Anomalonema sp.									x			
Paleolimnadiopsis sp.	x	x	x		x	x		x				x
Hemicycloidea tricarinata (Meek & Worthen)										x		x
Hemicycloidea ashleyi Raymond												x
Carbonita sp.								x				
Ostracoda undetermined				x		x	x		x		x	
Lepidoderma sp.												x
Xiphosura sp.					x	x						
VERTEBRATA												
Fish teeth	x		x				x					x
Fish scales	x		x			x						x

TABLE 2—ENVIRONMENTAL FAUNAL CLASSIFICATION

Faunal Group	Index Fossils	Rock Type	Associated Genera	Inferred Environment
4	Estherids	Shale and silty shale, med. dark-gray, laminated with platy siderite.	*Estheria,* Leaia,** Anthraconauta, Xiphosura, Lepidoderma, Carbonicola Plant fossils.*	Fresh-water
3	Phosphatic brachiopods and pectenids	Shale and silty shale, black to dark-gray, fissile to platy, nodular siderite concretions.	*Lingula, Dunbarella Aviculopecten, Orbiculoidea, Anthraconauta.*	Restricted marine or near-shore marine.
2	Calcareous brachiopods	Shale, dark-gray with nodular siderite concretions.	*Chonetes, Marginifera, Composita.*	Marine
1	Calcareous brachiopods, cephalopods, pelecypods, and gastropods	Shale, dark-gray to gray-black, poorly bedded, soft with thin, dark, limestone lenses.	*Marginifera, Chonetes, Mesolobus, Composita, Linoproductus, Meekospira, Sphaerodoma, Euphemites, Lophophyllum, Pseudorthoceras.*	Marine

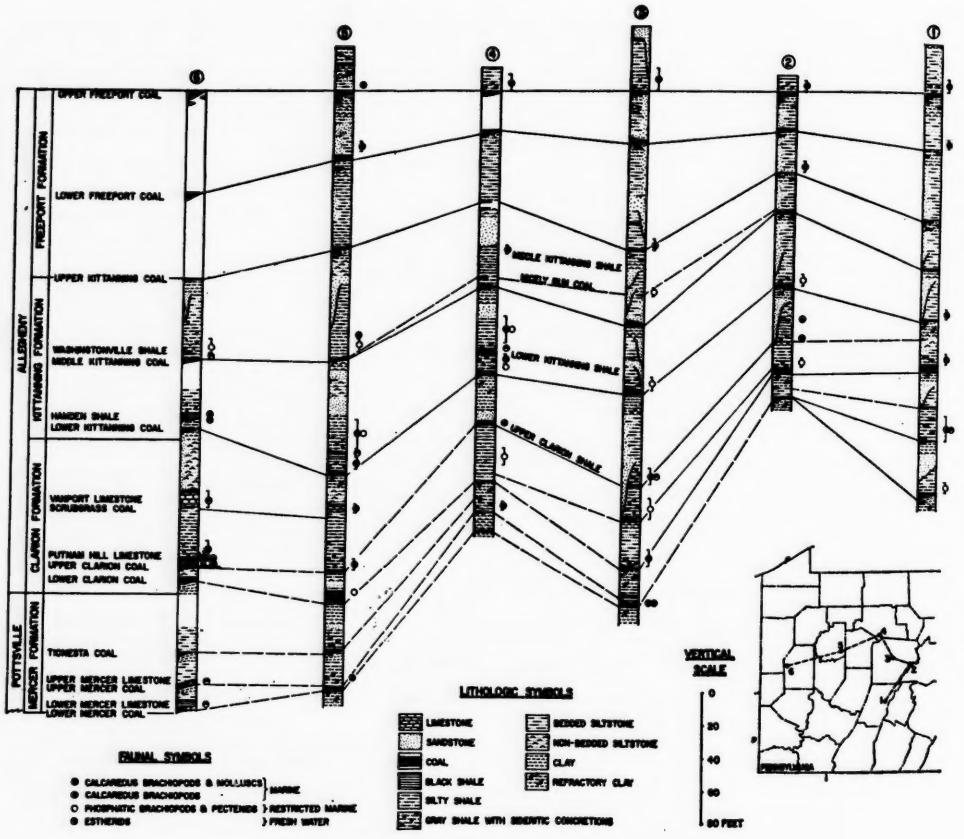
* *Estheria* = *Paleolimnadiapsis.*
** *Leaia* = *Hemicycloidea.*

River area which is the type area for the Allegheny group and for most named Allegheny coals. The type area for the Mercer coals and associated marine limestones is in the Beaver Valley region, represented by section 6. The type region for all marine shales and limestones in the Allegheny is in eastern Ohio or extreme western Pennsylvania. This area is also represented by section 6.

Regional correlations are based upon the stratigraphic position and order of occurrence of the most persistent beds, which are the fossiliferous marine shales and limestones, and fresh water limestones. In each section shown in text-fig. 3, these various beds are restricted in number and stratigraphic position. The fossiliferous marine or restricted marine beds vary in number from two to six and occur in the lower and middle parts of the sections. No more than six marine beds have been observed in any one section. In complete sections, three fresh-water limestones are present immediately below the upper three coals. The lowest fresh-water limestone is stratigraphically above the highest marine bed.

The limited number of marine beds and fresh-water limestones and their consistent order of occurrence from section to section is evidence for the gross aspects of the correlations presented in text-fig. 3. The most important of these correlations are listed and discussed below:

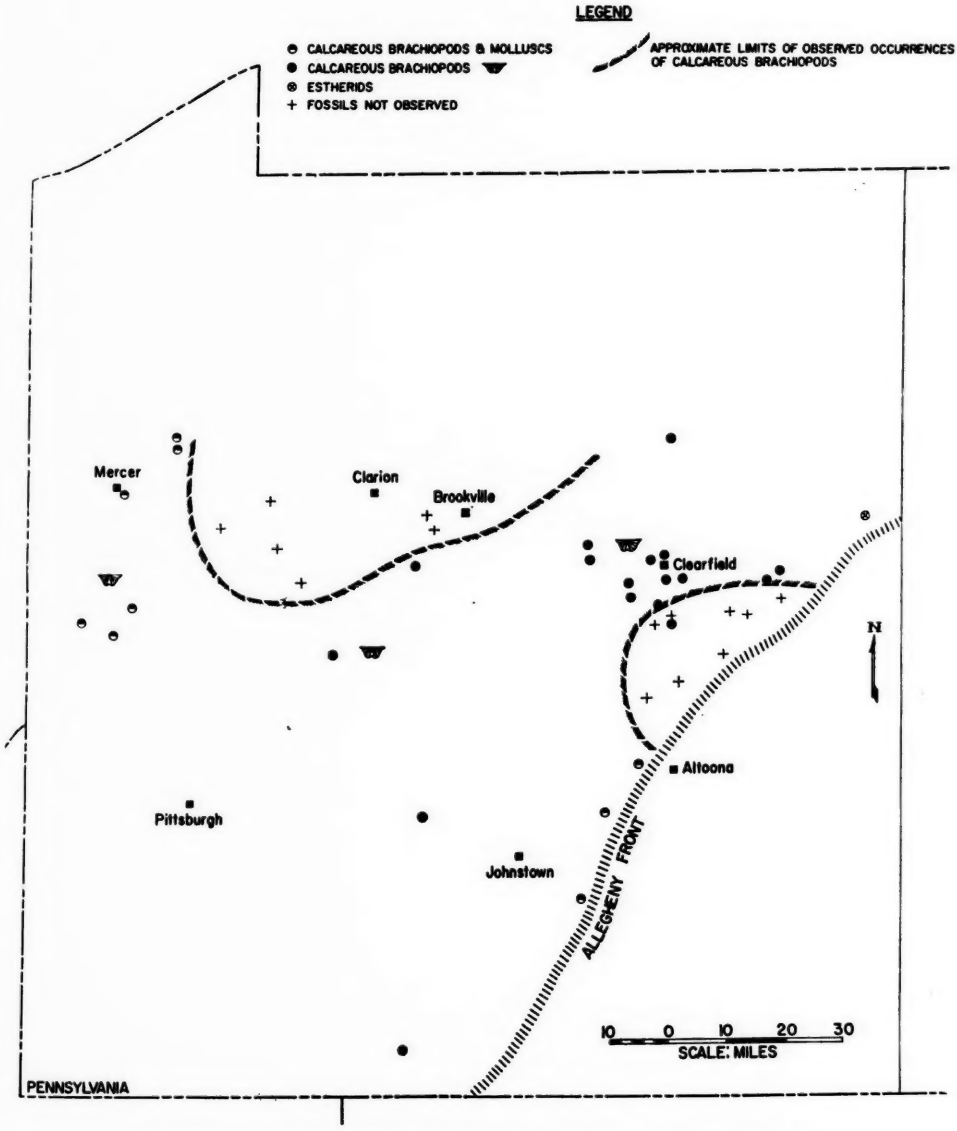
1. The marine shale which overlies the Middle Kittanning coal in the Allegheny type area, section 5, is correlated with the marine Washingtonville shale of section 6. This correlation has been postulated by Ferm (1957). In areas further east of the Allegheny River, the Middle Kittanning coal splits and the marine bed then lies above the upper coal called by Ferm (1957) the Nicely Run. The highest bed containing restricted marine fossils in sections 2 and 3 is correlated with the marine Washingtonville of the western sections.
2. The marine shale above the Lower Kittanning coal in sections 4 and 5 is correlated with the Hamden marine shale of the Beaver Valley area, section 6. This correlation has been posulated by Ferm (1957). In sections 2 and 3 restricted marine fossils replace the marine ones and in section 1 only fresh water fossils have been observed.
3. Correlation of the marine Vanport limestone between the Beaver River and Allegheny River areas presents no particular problem but the limestone is seldom observed east of Jefferson County. It is believed that the larger siderite concretions containing marine fossils, which occur about half way between the Lower Kittanning and Upper Clarion coals in section 2 represent the eastern equivilent of the Vanport. These concretions



TEXT-FIG. 3—Regional correlation diagram.

were first described by Williams & Nickelsen (1958).

4. The Putnam Hill marine limestone and shale of section 6 is correlated with the marine shale above the Upper Clarion coal in section 5, the type area for the Clarion coals. If this correlation is correct, the coal mapped as Brookville by De Wolfe (1929) and others in the Beaver Valley area is probably the Lower Clarion coal or the combined Upper and Lower Clarion coals. Ashley, in unpublished work quoted by Shaffner (1946, p. 48) expressed the same belief.
5. The Lower Clarion Coal in its type area, section 5, is overlain by shale containing restricted marine fossils. This bed has not been recognized in sections to the west but has been observed in sections 2, 3 and 4 to the east. In sections 2 and 3, the coal underlying the shale containing the restricted marine fossils has been mapped by Ashley (1940) as Brookville. However, it is believed that this coal is the Lower Clarion.
6. The lowest marine bed in sections 1 to 5 is believed, on the basis of stratigraphic position, to correlate with the Upper Mercer limestone of the Beaver River area, section 6.
7. The Brookville coal (second coal from the bottom in section 5) in the type area is not associated with any marine beds or other distinctive rock types. Therefore correlation of this coal is difficult. On the basis of stratigraphic position with respect to the Mercer and Clarion coals and marine beds, the Brookville is correlated with the Tionesta (Homewood) coal of section 6. The coal occurring is the same stratigraphic position in all eastern sections is also believed to be the Tionesta. Because the name Brookville has been applied to several stratigraphically different coal beds and because coals are difficult to recognize at this

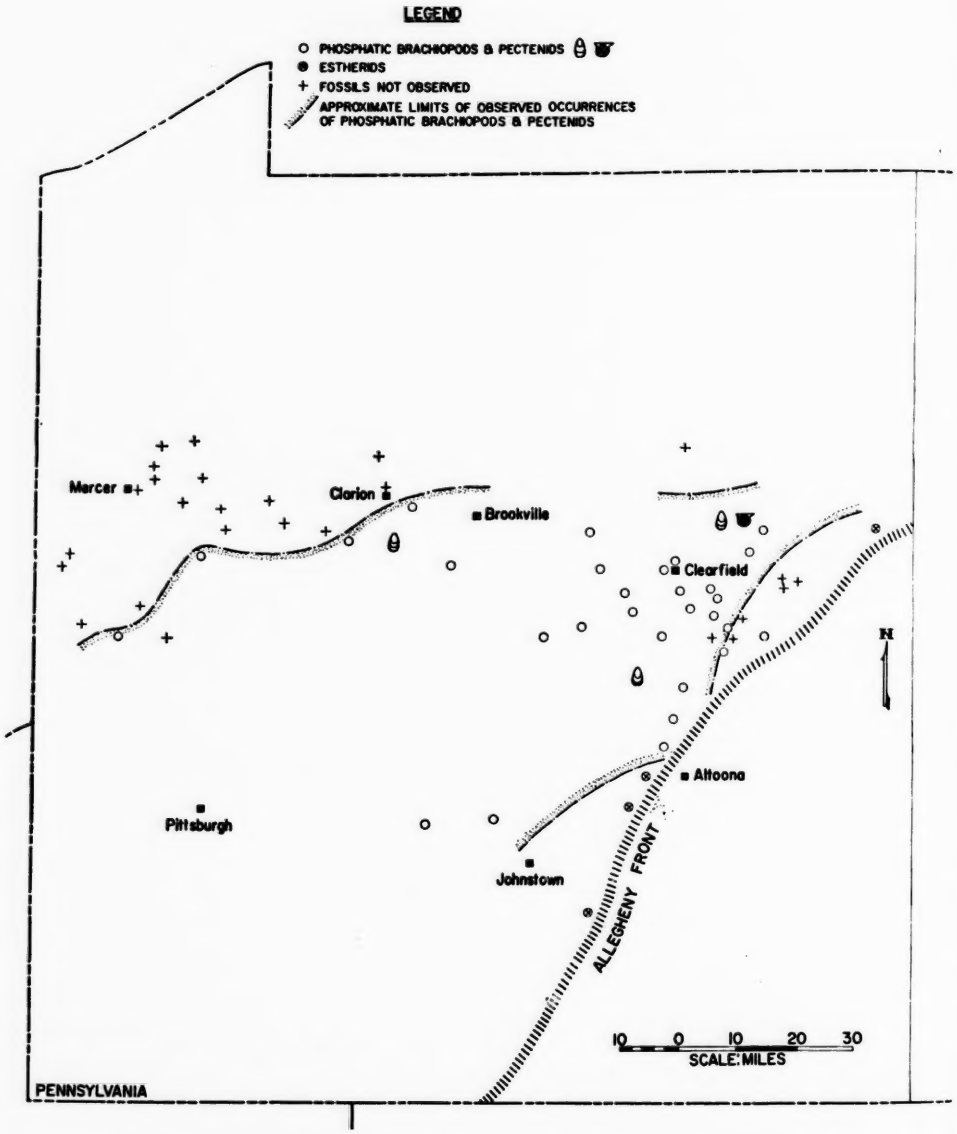


TEXT-FIG. 4—Distribution of faunas in shales above Upper Mercer Coal.

position, the designation of the Brookville coal as the Allegheny-Pottsville boundary is not satisfactory (Ashley, 1945). For this reason, among others, Ashley advocated placing the Allegheny-Pottsville boundary at the base of the Lower Kittanning coal, or clay, As shown in text-fig. 3, the writer places this boundary at the base of the Lower Clarion clay on the basis that this is the underbed of the lowest, consistently recognizable coal in the lower Pennsylvanian of western Pennsylvania.

DISTRIBUTION OF FAUNAS

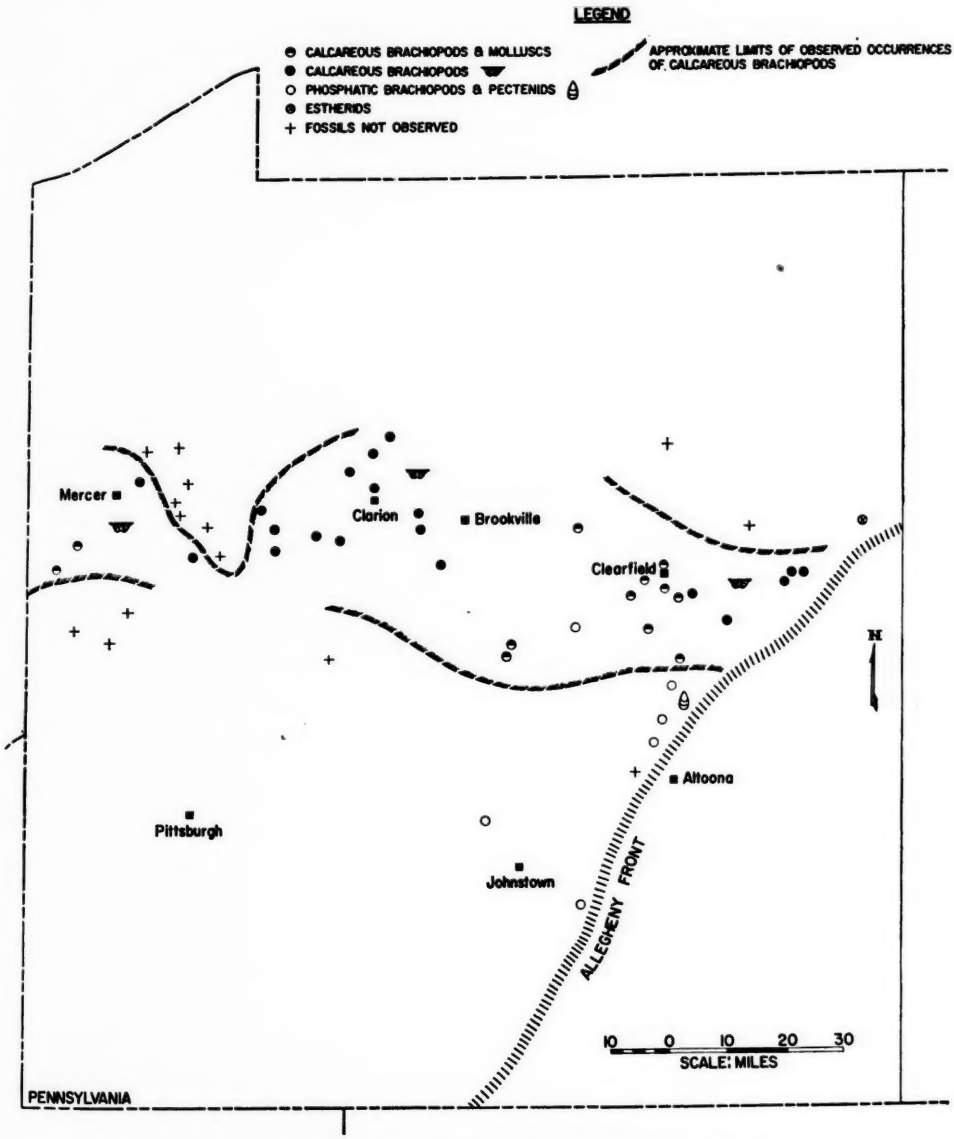
Dunbar & Condra (1932) have discussed the use of environmental faunal assemblages in correlation of Pennsylvanian sediments.



TEXT-FIG. 5—Distribution of faunas in shales above Lower Clarion Coal.

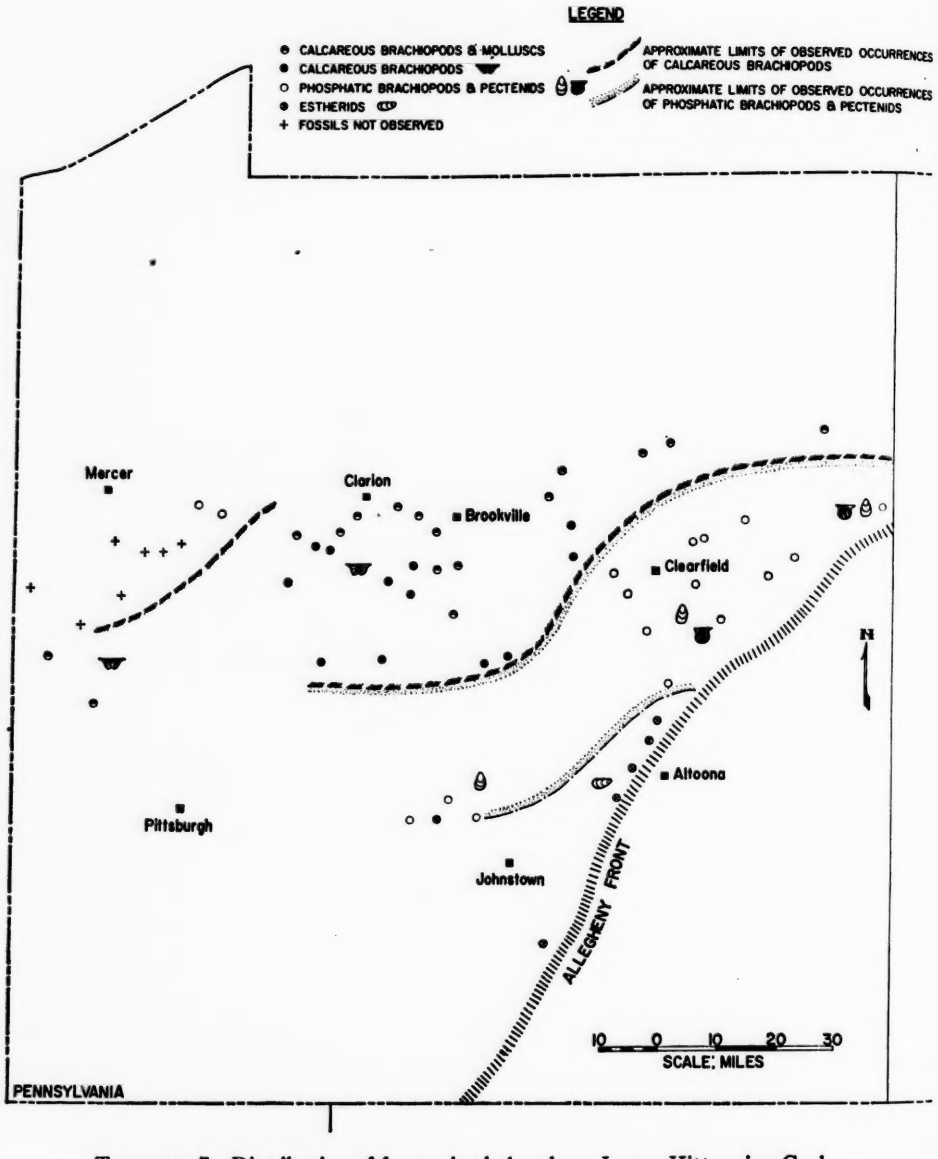
They conclude that such assemblages may be quite useful for precise regional correlations if a relatively large number of zones are used and if simultaneous estimates are made of the lateral faunal variation. Such faunal changes can best be shown on maps.

Maps of faunal variability in a given thickness of rock may be constructed in several ways. One method is to determine by statistical procedures involving ratios of genera or species the total faunal aspect of the selected interval at various localities. Maps expressing faunal variation determined in this way are called "biofacies



TEXT-FIG. *6*—Distribution of faunas in shales above Upper Clarion Coal.

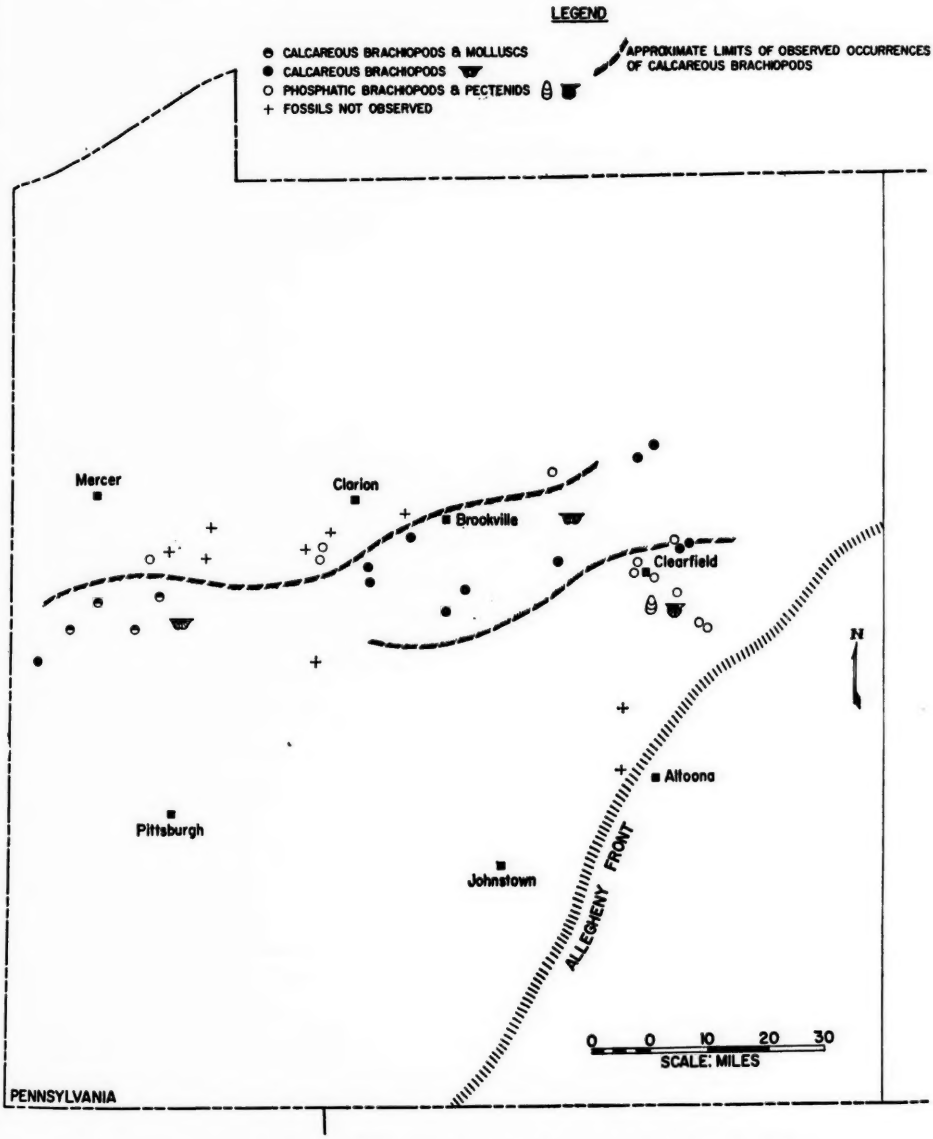
maps." Use of this method requires more intensive sampling and analytical techniques than could be attempted in this investigation. Another, simpler method, is to determine the presence or absence of selected groups of fossils. This procedure, which was used in this study, consists of determining for each section the vertical range and stratigraphic position of the various faunal groups shown in table 2 and plate 121. If more than one group is present, the most marine or deepest-water marine group is placed on the map. Such maps represent the faunal variability at the time of maximum marine sub-



TEXT-FIG. 7—Distribution of faunas in shales above Lower Kittanning Coal.

mergence. In some places no fossils were found in the various shale beds studied. Therefore, in addition to the four faunal groups shown in table 2, a fifth class was added, namely "absence of fossils." The absence of fossils does not necessarily imply continental origin.

Faunal distribution maps for all marine, fossiliferous beds except the Vanport limestone in the Pottsville and Allegheny groups of western Pennsylvania, and which occur stratigraphically below the Upper Kittan-



TEXT-FIG. 8—Distribution of faunas in shales above Middle Kittanning Coal.

ning coals are shown in text-figs. 4,5,6,7 and 8. The following conclusions are obtained from these maps:

1. For all mapped fossiliferous beds, marine or restricted marine fossils are distributed across the width of the Allegheny Plateau region, from the Ohio border on the west to the Allegheny Front on the east.
2. In the Upper Mercer and Lower Clarion shales, (text-figs. 4,5), the marine or restricted marine fossil areas are generally bounded on the north and east by areas where invertebrate fossils have not been found.
3. In the Upper Clarion, Lower Kittanning and Middle Kittanning shales (text-figs. 6,7,8), the areas of marine fossils extend as east-

west or northeast-southwest trending belts across the central part of the plateau area. They are bounded on the northwest and southeast by areas of restricted marine or fresh-water fossils or areas in which fossils have not been found.

4. The most complete faunal transition, from deepest marine to fresh-water fossils is found in the Lower Kittanning shale (text-fig. 7).

APPLICATIONS OF MAPS

The faunal distribution maps (text-figs. 4–8) have two main uses. The first is to aid in the more precise identification of the economically important coal and clay beds which are associated with the fossiliferous beds, and the second is to obtain a better understanding of Pennsylvanian paleogeography. Applications of the maps for either purpose assumes that the various fossiliferous beds and associated sediments have been correctly correlated. The validity of this assumption has been discussed.

In some areas of study, the maps may be used to identify individual coal beds. For example, in the vicinity of Clarion, calcareous brachiopods and molluscs (group 1) are found in shales above the Lower Kittanning Coal (text-fig. 7). Examination of the other maps will show that this faunal group does not occur in shales above any of the other Allegheny or Pottsville coals in this area. In view of these facts, a coal in the vicinity of Clarion overlain by shales containing calcareous brachiopods and molluscs would be identified as the Lower Kittanning. If a brachiopod assemblage without molluscs (group 2) is found in shales above a coal in the same area, then, by similar reasoning, the coal would be identified as the Upper Clarion. For other coals and in other areas, use of the maps may reduce the identification to several alternatives, which must be resolved by other criteria, usually stratigraphic position or the order of occurrence.

Based on the environmental interpretations of fossils shown in table 2, and the geographic distribution of fossils shown in text-figs. 4–8, some tentative paleogeographic conclusions are made.

1. During Upper Pottsville and Allegheny time, six marine invasions entered Pennsylvania and extended in an approximate east-west or northeast-southwest direction across the Allegheny plateau area.
2. The lowest two marine invasions, the Upper Mercer and Lower Clarion, were bounded on the north and east by continental or restricted marine areas of sedimentation.
3. The last four marine invasions, the Upper Clarion, Vanport, Lower Kittanning and Middle Kittanning, extended as relatively narrow embayments across the region of the Allegheny Plateau, and were bounded on the north-west and south-east by areas of continental or restricted marine sedimentation. The conclusions concerning the distribution of the Vanport limestone are based on the work of Swain (1946).
4. The fact that all the marine, fossiliferous beds are bounded on the northwest, north, east and southeast by rocks which contain fresh-water fossils or no invertebrate fossils would suggest that the sediments which filled the marine basins were derived from these directions. In other words, the seas advanced from the west or southwest and were filled with sediment transported from the north, east and south. These conclusions are supported in part by cross-bedding studies (Williams, 1959.)

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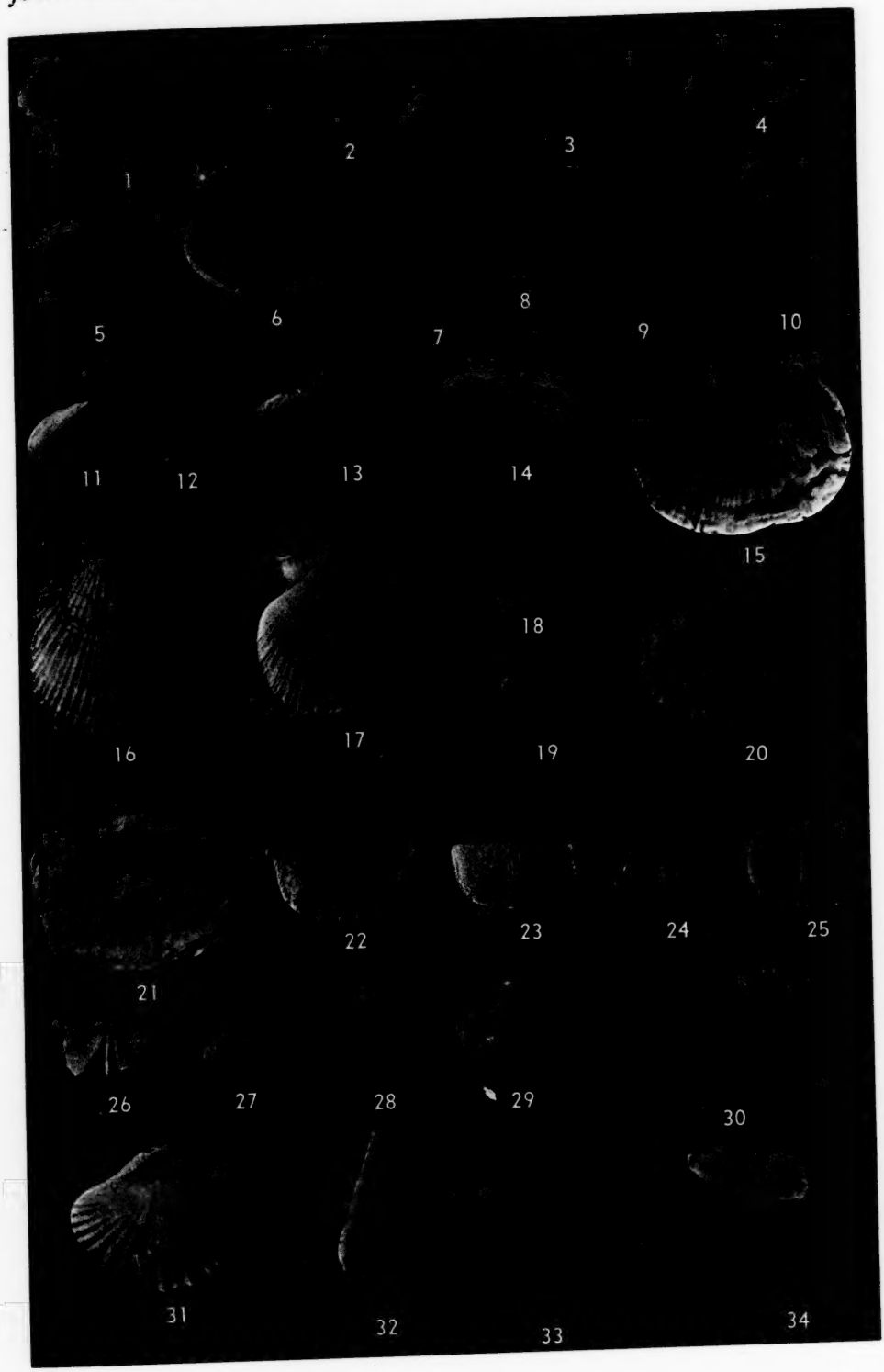
(*Explanation of* PLATE 121 *on next page.*)

EXPLANATION OF PLATE 121

FIGS. *1–6—FRESH-WATER FOSSILS. 1,2, Paleolimnadiopsis sp.* External molds from Upper Freeport shale, 2 miles south of Clearfield, Pa.; ×4. *3–5, Hemicycloidea tricarinata* (Meek & Worthen). External molds, somewhat deformed, from Upper Freeport shale near Coalport, Pa.; ×4. *6, Anomalonema sp.* External mold from Upper Kittanning shale, 1 mile north of Clearfield, Pa.; ×4.

7–19—RESTRICTED MARINE FOSSILS. 7,8, Lingula carbonaria Shumard. Ventral views of small and medium sized specimens from Lower Kittanning shale at Clearfield, Pa.; ×2. *9,10, Orbiculoidea missiouriensis* (Shumard). Partly exfoliated dorsal and ventral valves from Lower Clarion shale, 1 mile northeast of Clearfield, Pa.; ×2. *11,12, Anthraconauta minima* (Ludwig). External views of left valves from Lower Kittanning shale, 8 miles south of Punxsutawney, Pa.; ×2. *13,14, Anthraconauta phillipsi* (Williamson). Exterior views of right and left valves from Lower Kittanning shale at Luthersburg, Pa.; ×2. *15,16, Dunbarella whitei* (Meek). Exterior views of left and right valves from Lower Clarion shale at Clearfield, Pa.; ×2. *17, Aviculopecten occidentalis* (Shumard). Exterior view of left valve from Lower Kittanning shale at Corsica, Pa.; ×1. *18,19, Aviculopecten eaglensis* (Price). External molds of left and right valves from Upper Mercer shale near Clearfield, Pa.; ×4.

20–34—MARINE FOSSILS. 20,21, Marginifera muricatina Dunbar & Condra. Ventral and dorsal views, from Lower Kittanning shale at Sligo, Pa.; ×2. *22,23, Chonetes granulifer* Owen. Interior molds of ventral valves from Lower Kittanning shale, 1 mile south of Brockway, Pa.; ×2. *24,25, Mesolobus mesolobus* var. *decipiens* (Girty). External views of ventral valves, Upper Clarion shale, 8 miles south of Punxsutawney, Pa.; ×2. *26,27, Mesolobus mesolobus* var. *lioderma* Dunbar & Condra. External views of ventral valves from Lower Kittanning shale at Corsica, Pa.; ×2. *28,29, Composita argentea* (Shepard). Ventral and dorsal views, from Vanport limestone, 8 miles south of Punxsutawney, Pa.; ×2. *30, Linoproductus prattenianus* (Norwood & Pratten). External mold of dorsal valve from Lower Kittanning shale at Benezette, Pa.; ×1. *31, Spirifer opimus* Hall. Dorsal view, from Vanport limestone, 4 miles west of Brockway, Pa.; ×2. *32, Meekospira sp.* Exterior view, from Lower Kittanning shale at Monaca, Pa.; ×4. *33, Sphaerodoma brevis* White. Exterior view, from Lower Kittanning shale at Benezette, Pa.; ×2. *34, Lophophyllum profundum* (Milne-Edwards & Haime). Fragmental specimen from Vanport limestone, 4 miles West of Brockway, Pa.; ×2.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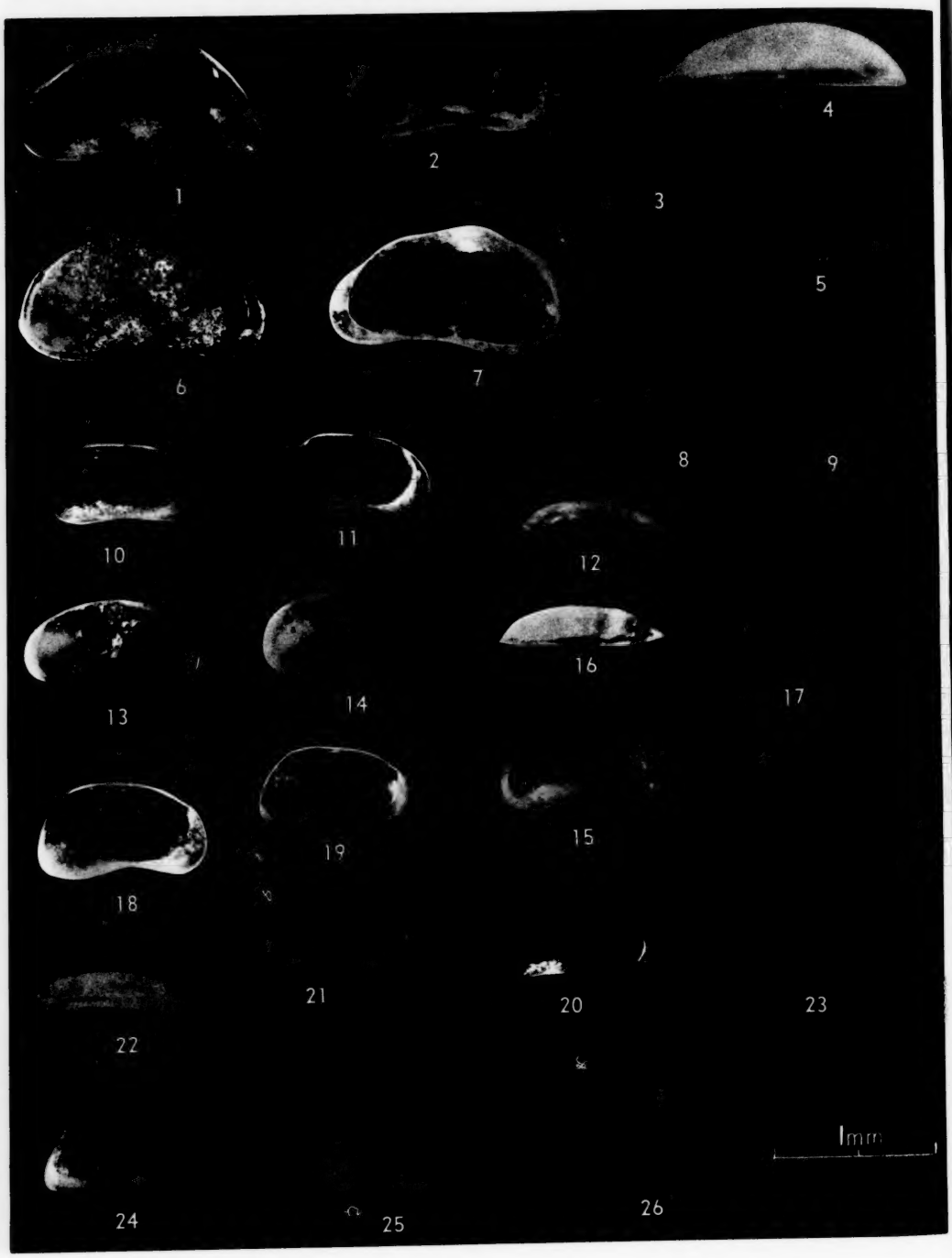
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JOURNAL OF PALEONTOLOGY, V. 34, NO. 5, P. 923–932, PLS. 122–123, SEPTEMBER, 1960

POST-PLEISTOCENE OSTRACODES OF LAKE NIPISSING AGE

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ABSTRACT—A small ostracode fauna is described from lake silts about 4000 years old of Lake Nipissing age from Bear Cave, Michigan. Seven genera and fourteen species were found, three of which are new. About half of these species were previously described as populating temporary ponds although the lake was a deep, permanent lake with moderate water temperatures.

INTRODUCTION

A SMALL ostracode fauna is described from Bear Cave, which is located about three and one-half miles north of Buchanan, Michigan (SW¼, NW¼, sec, 12, T7S, R18W, of the Niles, Michigan quadrangle). The geology of Bear Cave was described in more detail by the author previously (15). The cave is located in tufa deposits which grade into silty lake beds at the base, gray to yellowish in color and between one to ten inches thick. The thin lake beds are underlain by coarse gravel and sand. Samples were taken from three different horizons of the silt layer. A rich fauna of ostracodes, besides freshwater gastropods and clams, was washed from the silt, most of it from the lower beds. The upper part of the profile is marked by a deep red band of tufaceous material firmly cemented with limonite; at this point the clayey silt grades into the overlying tufa. The washed residue of the silt shows numerous fence-like limy concretions which higher up in the profile combine to form the tufa. Some additional ostracodes were recovered in a soft pocket of partially disintegrated tufa in an exposure outside of the cave.

The age of the silt probably corresponds to the Lake Nipissing stage of ancient Lake Michigan. This stage at 595 feet followed the Lake Chippewa low water stage in which time, probably for the duration of about 4000 years, the St. Joseph River rejuvenated its channel through glacial drift down to the bedrock and dammed up a lake upon rising again to the 595 foot level of Lake Nipissing. It was a long and deep lake, probably with shallow shores, muddy bottom and moderate vegetation. Much lime was available in the water of the Bear Cave area as numerous tiny branch-like concretions were formed in the silt, especially in the upper section where it continues into massive tufa banks. The author believes that the entire profile of about ten inches of

EXPLANATION OF PLATE 122

FIGS. *1–5—Candona crogmaniana* Turner. *1*, right valve, inside; *2*, right valve, outside; *3*, left valve, dorsal view; *4–5*, right valve, dorsal view.

6–9—Candona decora Furtos. *6*, right valve, outside view; *7*, right valve, inside view (infrared); *8*, dorsal view; *9*, muscle scars.

10–12—Candona fossulensis Hoff. *10*, right valve, outside view; *11*, left valve, inside view; *12*, left valve, dorsal view.

13–17—Candona poseyensis Staplin, n. sp. *13*, left valve, outside view; *14*, left valve, inside view; *15*, left valve, dorsal view; *16*, right valve, inside view, young instar; *17*, muscle scar patterns.

18–23—Candona scopulosa Furtos. *18*, right valve, outside view (infrared photo); *19*, left valve, inside view, genital lobes visible; *20*, left valve, outside of elongate shell; *21*, right valve, dorsal view; *22*, muscle scars; *23*, left valve, outside view, early instar.

24–26—Candona sigmoides Sharpe. *24*, left valve, inside view; *25*, left valve, outside view; *26*, left valve, dorsal view.

silt and about 15 feet of tufa was deposited within Nipissing time, which probably lasted 1500 years. Zumberge & Potzger (1956) described two pollen profiles from the area of South Haven, Michigan, which is located only about 50 miles north of Bear Cave. The pollen profiles show a temperature optimum at Nipissing time since the end of the last ice retreat (Xerothermic), which fact must have resulted in lake temperatures similar to or even higher than those of the present. The water was probably fairly clear and spring fed in the vicinity of Bear Cave.

The present information on Pleistocene and Post-Pleistocene ostracodes is very much limited; the literature being scarce and scattered. The most important information on Pleistocene ostracodes of central North America is Staplin's unpublished thesis which is expected to be published within a short time. Publications by Hucke (1913), Luettig (1955), and Wagner (1957) describe Pleistocene ostracodes in Europe; however, their species are, for the most part, unknown in North America. The identification of the Bear Cave material was difficult, therefore, and had to be based on subarctic and subtropical living forms. Authors like Furtos (1933, 1935, 1936), Bronstein (1947), and Hoff (1942), emphasized the structure of the soft parts and neglected the morphology of the carapace. The key illustrations of the mentioned authors are simplified inaccurate line drawings. As no soft parts are available with the fossil material, the author illustrates each species in side view, both inside and outside and the dorsal view. Muscle scar patterns are added where visible although their taxonomic role is not quite understood yet, and thus, their value is still limited. For better transparency of translucent shells in some cases, infrared sensitive film was used in connection with a Wratten A, No. 25 filter; however, the very coarse grain of infrared film materials does not recommend a general use for microfossil photography. The preservation is generally very good as the process of fossilization has hardly started yet. Large thin-shelled forms broke during the washing process. The silt easily slakes in water if air dried.

The author is in doubt if the establishment of stratigraphic horizons is possible with the help of ostracodes as the late Pleistocene epoch is geologically too short to develop genetic changes. They certainly should give information on the environments, e.g., average water temperatures, depth, size and permanence of the water body. A study of the tolerance of recent ostracodes to their environments would be a considerable help for the understanding of Pleistocene ostracodes.

The description of ostracodes had to be limited to the morphology of the carapaces as no soft parts were found preserved. The problem of the dimorphism of a new species or a strong bivalval difference created a major problem. The author made the attempt to minimize the naming of new genera and species and ascribed deviations of the shape to local variation rather than new species.

SYSTEMATIC DESCRIPTIONS

Order OSTRACODA Latreille 1802
Family CYPRIDAE
Subfamily CANDONINAE
Genus CANDONA Baird 1845
Pl. 122, figs. 1–5

CANDONA CROGMANIANA Turner

Candona crogmaniana Turner, 1894, p. 20–21, pl. 8, figs. 24–33; Furtos, 1933, p. 476, pl. 8, figs. 1–3, pl. 9, figs. 17,18, pl. 11, p. 9–10; Hoff, 1942, p. 79–80, pl. 3, figs. 31,32.
Candona crogmani Turner, 1895, p. 300–301, pl. 7, figs. 24–33, pl. 8, figs. 4,5; Sharpe, 1198, p. 824, fig. 1295a,b,c.

Side view.—Shell subtriangular, greatest height near posterior third, less than half the length; anterior extremity rounded, gently ascending to dorsal margin; dorsal margin continues straight at first third after slight break, descending again after second break near second third; posterior extremity pointed; ventral margin slightly sinuated at second fifth from anterior end; inner margin strongly developed around anterior extremity, about 0.15 mm. wide narrowing to less than 0.1 mm. at the ventral margin.

Dorsal view.—Shell of compressed elliptical outline; right valve overlaps left narrowly along dorsal margin protruding with a prong-like extension near anterior end, overlapping more extensively with another prong near posterior end; shell smooth and transparent with a few scattered pore canals.

Dimensions.—

Length	Height	H/L	Width
1.27	0.63	0.49	
1.53	0.72	0.52	0.44

Remarks.—A total of three forms was found in the lower part of the silt. Both the size and the shape closely correspond to the Hoff (1942) and Furtos (1933) forms. It is not quite clear if *Candona decora* Furtos (1933), separately described below, is the male form of *Candona crogmaniana*. According to Furtos' illustration, the male is very different from that of the author's. Staplin's form is much more elongate, the male corresponds more to *Candona decora* Furtos 1933.

Ecology.—Turner (1894) collected his type specimen from a shallow pond near Atlanta, Georgia. Furtos (1933) collected this species from both vernal and permanent ponds and Hoff (1942) from a permanent oxbow lake from floating algae in Illinois.

CANDONA DECORA Furtos
Pl. 122, figs. 6–9

Candona decora Furtos, 1933, p. 477, pl. 8, figs. 4,5, pl. 9, figs. 21,22, pl. 11, figs. 5,6.

Side view.—Shell subtriangular, height greatest in posterior third, less than half the length; anterior extremity rounded, dorsal slope gently ascending to dorsal margin; slight break after first third to continue in a straight line to the highest point of the shell before second third, slight sinuation after hump for broadly rounded posterior extremity; ventral margin with slight sinuation near second fifth from anterior end; inner margin about 0.15 mm., strongly developed around anterior extremity, narrowing at the ventral margin to less than 0.1 mm.; shell translucent and smooth with a few scattered pore canals.

Dorsal view.—Shell compressed elliptical, anterior end more pointed than posterior, dorsal prongs only weakly developed which overlap left shell.

Dimensions.—

Length	Height	H/L	Width
1.50	0.80	0.53	0.25

Remarks.—This form may be possibly the male of *Candona crogmaniana* Turner 1894. Furtos (1933) pictured the male to *Candona crogmaniana* with an antero-ventral hump, typical for some Candona males; however, with a different outline of the dorso-posterior part and the posterior extremity. Staplin illustrates his *Candona crogmaniana* male identical with the author's specimen. The author has the impression that the available shell rather belongs to the species *Candona decora* Furtos (1933) than to *Candona crogmaniana* Turner (1894).

Ecology.—Furtos describes the occurrence of this form as rare in small ponds and lakes in April.

CANDONA FOSSULENSIS Hoff
Pl. 122, figs. 10–13

Candona fossulensis Hoff, 1942, p. 92, pl. 5, figs. 58–64.

Side view.—Shell subquadrate with anterior extremity well-rounded, posterior extremity broadly rounded; dorsal slope steeply ascending from anterior end running nearly parallel to ventral margin; break of dorsal slope at first third to nearly straight line, slightly ascending to second third, then dropping off after a clear break, first mildly and then rapidly to the posterior extremity; height larger than half the length; ventral margin nearly straight with slight sinuation in center portion. Inner margin about 0.16 mm. at anterior extremity, very narrow at posterior end; shell smooth with a few scattered pore canals, nearly transparent. No sexes could be distinguished.

Dorsal view.—Shell flatly compressed.

Dimensions.—

Length	Height	H/L	Width
0.95	0.52	0.55	0.20
0.91	0.47	0.52	
0.88	0.45	0.51	
0.95	0.53	0.56	

Remarks.—The outline of this form is very similar to that of *Candona scopulosa;* however, the outline of the top view and the curvature of the posterior extremity differ considerably. Hoff (1942) gives lengths of 0.99–1.06 and heights of 0.52–0.57 for the female; 1.12–1.20 and 0.59–0.64 for the male. The variability of this species is moderate. A few specimens show male genital lobes faintly; this fact excludes the possibility of this species being the female to *Candona scopulosa.*

Ecology.—Hoff (1942) found this species in a roadside ditch with dead grass in vernal ponds.

CANDONA POSEYENSIS Staplin, n. sp.
Pl. 122, figs. 13–17

Staplin named and described this species in his thesis. It is here published and credited to him.

Side view.—Shell elliptical elongate with both extremities well-rounded; greatest width first third from posterior end, a little greater than width near anterior end; dorsal margin slightly sinuated about two-fifths from anterior end; anterior extremity narrower rounded than posterior; inner margin narrow at both ends not exceeding a width of 0.1 mm.; shell smooth and transparent with very few pore canals.

Dorsal view.—Shell elliptical compressed, pointed anteriorly and steeply rounded posteriorly; slight prongs along dorsal margin of left valve at first and last fifth of length which overlap and accept right valve.

Dimensions.—

Length	Height	H/L	Width
1.10	0.55	0.50	0.26
0.90	0.45	0.50	
1.05	0.53	0.50	
1.12	0.54	0.48	
0.72	0.34	0.47	
0.96	0.44	0.46	
0.94	0.45	0.48	
0.99	0.46	0.47	
0.72	0.34	0.47	

Remarks.—This form does not appear to be related to any other *Candona* described in the literature.

Ecology.—Staplin found this form together with *Limnocythere verrucosa* and *Candona truncata*. Both forms are inhabitants of vernal and permanent ponds with moderate organic matter.

CANDONA SCOPULOSA Furtos
Pl. 122, figs. 18–23

Candona scopulosa Furtos, 1933, p. 479, pl. 8, figs. 7–10, pl. 12, figs. 11–13. Staplin, 1952.

Side view.—Shell subquadrate with well-rounded anterior extremity; dorsal margin gently curved with a small break near the first third, another break near the second third before posterior slope to extremity; dorsal curvature very gentle between first and second third; posterior end angular enclosing about 80 degrees between dorsal and ventral margin; ventral margin interrupted by gentle sinuation; inner margin generally narrow except around posterior extremity where it reaches about 0.18 mm. width; genital lobes clearly visible, as apparently only males were found; shell thin and transparent with scattered pore canals.

Dorsal view.—Shell elliptical with some tumidity.

Dimensions.—

Length	Height	H/L	Width
0.97	0.53	0.55	0.27
0.92	0.52	0.56	
0.93	0.52	0.56	
0.98	0.54	0.55	
0.95	0.52	0.55	
0.98	0.54	0.55	
0.96	0.54	0.56	
0.95	0.52	0.55	
0.92	0.50	0.54	
0.95	0.53	0.56	
0.88	0.51	0.58	

A large number of smaller forms were found with very similar outlines but greater elongation. It is not clear if this is a young instar to *Candona scopulosa* as no genital markings of any kind are visible in these shells.

Dimensions.—

Length	Height	H/L
0.82	0.41	0.50
0.72	0.35	0.49
0.74	0.35	0.48
0.69	0.39	0.52
0.78	0.37	0.48

Remarks.—*Candona scopulosa* displays a remarkable variety of shapes. Furtos' (1933) illustrations of male and female approximately correspond to the author's specimens. It is questionable if the young instars described here are females with either invisible or still undeveloped sexual markings. The form is very common and its shape varies a little.

Ecology.—Furtos describes this species as common along the rocky shores and in shallow rock pools of Lake Erie, occasionally in weedy inlets and marshes connected with the lake from May to August.

CANDONA SIGMOIDES Sharpe
Pl. 122, figs. 24–26

Candona sigmoides Sharpe 1897, p. 455–456, pl. 45, figs. 4–11; Hoff, 1942, p. 82–84, pl. 3, figs. 36–38.

Side view.—Shell subquadrate, height about half the length; anterior extremity broadly rounded; ascending slope nearly straight with a mild break to straight dorsal margin at first third which falls off steeply

after stronger break beyond second third to beak-like posterior extremity; ventral margin straight with clear sinuation halfway towards posterior end; small hump beyond sinuation and steeply arched posterior extremity; inner margin narrow; shell smooth with a few scattered pore canals.

Dorsal view.—Shell trapezohedral, with a clear break about one third from anterior and a minor break near posterior end.

Dimensions.—

Length	Height	H/L
0.89	0.46	0.52
0.91	0.48	0.53
0.92	0.48	0.53
0.92	0.48	0.52
0.92	0.48	0.52
0.94	0.48	0.51
0.92	0.51	0.55
0.94	0.49	0.52
0.88	0.45	0.51

Remarks.—This material is much smaller than the same specific material described by Hoff (1942). His dimensions range from 1.02–1.06 for the length and 0.52–0.54 for the height for female specimens; 1.20 and 0.61 for males. This form is clearly different from *Candona sigmoides* in outline and index ratio (H/L).

Ecology.—Sharpe described this species from lake and river shores. Hoff (1942) found it hanging in weeds of permanent lakes and in slow current of small permanent streams.

Subfamily CYPRINAE
Genus CYPRIA Zenker
CYPRIA NIPISSINGAE, n. sp.
Pl. 123, figs. 1–3

Side view.—Shell bean shaped, nearly of bilateral symmetry with the anterior part less broadly arched than the posterior; dorsal margin gradually ascending to highest point approximately in the middle of shell, descending at a less steep angle to a break about one-fifth from the posterior end, falling steeply to form the broadly rounded posterior end; ventral margin with slight sinuation in the center; muscle scar pattern characteristic for *Cypria* and *Cypridopsis;* shell smooth with a few pits under higher magnification; inner margin narrow.

Dorsal view.—Shell fairly tumid with greatest tumidity about one-third from posterior end.

Dimensions.—

Length	Height	H/L	Width
0.71	0.45	0.63	0.24
0.72	0.43	0.60	

Remarks.—This species has many generic properties in common with both *Cypria* and *Cypridopsis.* The only moderate tumidity and the lack of fine teeth on top of the dorsal arch seem to exclude the belonging to *Cypridopsis. Cypridopsis obesa* Brady & Roberts as pictured by Bronstein is closest to the writer's specimens. *Cypridopsis* has a broader arched anterior extremity and much wider inner margin. The writer's specimens are oriented the opposite way. There is also a certain similarity with *Potamocypris variegata* Daday 1900.

Ecology.—*Cypria* has a wide variety of environments ranging from a permanent lake to a weedy vernal pond.

Genus CYPRIDOPSIS Brady
CYPRIDOPSIS ELONGATA Kaufmann 1900
Pl. 123, figs. 4–7

Side view.—Shell elongate, bean-shaped, with the greatest height just behind the center of shell; greatest height a little higher than half the length; anterior margin narrowly rounded with the dorsal margin emerging from it with a weak curvature which is strong at the highest point where the dorsal margin descends first with a weak curvature to continue steeper to the broader posterior extremity; it is slightly pointed close to the ventral margin; ventral margin sinuated in center portion; inner margin wide at anterior extremity, very narrow around the other parts of the shell; shell smooth, sometimes reticulate.

Dorsal view.—Shell elliptical, slightly compressed and of intermediate tumidity, anterior end sharply pointed, posterior less pointed.

Dimensions.—

Length	Height	H/L	Width
0.57	0.30	0.53	0.15
0.57	0.32	0.56	
0.58	0.30	0.52	
0.56	0.29	0.52	
0.57	0.30	0.53	
0.60	0.31	0.52	
0.58	0.31	0.53	
0.58	0.31	0.53	
0.57	0.30	0.53	
0.53	0.28	0.53	
0.58	0.30	0.52	
0.57	0.29	0.51	

Remarks.—This species shows a great variety of the dorsal curvature and considerable difference in the roughness of the shell surface. It is believed that this form belongs to *Cypridopsis* although the genus *Cyprinotus* has a very similar muscle scar pattern. No other form could be located which was only approximately similar to the present common species. *Cypridopsis parva* G. W. Müller and *Cyprinotus inaequivalvis* Bronstein (1947) look similar; both forms are much higher.

Ecology.—*Cypridopsis elongata* is an inhabitant of permanent water bodies with some vegetation and moderate water temperatures.

Genus Cyprinotus
? Cyprinotus sp.
Pl. 123, figs. 8–10

Side view.—Shell subtriangular with a narrowly arched posterior and broadly arched anterior extremity; ventral margin nearly straight with a weakly sinuated center section; dorsal margin broadly curved anteriorly but nearly straight behind highest point which is narrowly curved; inner margin about 0.10 mm. wide at anterior end, about half the size at the posterior end; shell thin and smooth.

Dorsal view.—Shell compressed elliptical with both ends sloping about the same angle.

Dimensions.—

Length	Height	H/L	Width
0.72	0.41	0.57	0.18
0.69	0.50	0.61	
0.56	0.45	0.61	
0.57	0.34	0.60	

Remarks.—*Cypridopsis parva* Mueller as pictured by Bronstein is of a rougher surface and more tumid. No muscle scars are visible with any one of the author's specimens; thus, assigning this form to the genus *Cyprinotus* is questionable.

Ecology.—*Cyprinotus* is common in vernal ponds.

Genus Eucypris Vavra
Eucypris pigra Fischer
Pl. 122, figs. 11–14

Cypris pigra Fischer 1851
Cypris tumefacta Brady & Robertson 1870
Prionocypris tumefacta Kaufmann 1900
Eucypris pigra Müller 1912, Bronstein 1947, Luettig 1955

Side view.—Shell triangular, of bilateral symmetry; height larger than half the length; extremities well rounded, dorsal margin slightly curved to center point where it drops off at the same angle to posterior extremity; ventral margin sinuated; inner margin about 0.22 mm. wide at anterior end, narrow at posterior end; left valve seems to overlap right valve along dorsal margin; surface of shell covered with small tubercles.

Dorsal view.—Shell tumid and of helmet-like shape and of bilateral symmetry.

Dimensions.—

Length	Height	H/L	Width
0.99	0.53	0.54	0.34
0.98	0.56	0.57	
0.89	0.54	0.61	
0.96	0.53	0.55	

Remarks.—This form resembles very closely the specimens of Bronstein (1947) and Luettig (1955). The tumidity and the wide anterior inner margin are characteristic criteria for the genus *Eucypris*. The form occurs most frequently at the lower part of the silt.

Ecology.—Luettig found *Eucypris pigra* in ditches and cold springs with oxygen rich waters and with temperatures below +12°C., but the species is very resistant to higher temperatures.

Eucypris rava Furtos
Pl. 123, figs. 15–18

Eucypris rava Furtos, 1933, Ohio Biol. Surv., v. 5, p. 454–455, pl. II, figs. 13,14, pl. III, figs. 16,17. Bronstein, 1947.

Side view.—Shell subtriangular, well rounded anterior extremity; anterior slope ascends to highest point to a little less than the middle of the shell, posteriorly descends at about the same angle and slants off obtusely near the posterior extremity; extremity more acutely angled than anterior end; ventral margin nearly straight with slight sinuation opposite the highest point of shell; inner margin about 0.2 mm. wide becoming narrow on the ventral side; no inner margin along the dorsal margin; postero-ventral groove accepts margin of right valve.

Dorsal view.—Shell tumid with trapezohedran cross-section, the highest point in the anterior half, a lower hump in the posterior half.

Dimensions.—

Length	Height	H/L	Width
1.09	0.63	0.58	0.33
1.02	0.56	0.55	
1.26	0.66	0.52 (Furtos' 1933 specimen)	

Remarks.—*Eucypris rava* may easily be confused with *Cypricercus reticulatus* Sars 1928. The outlines of the shells resemble each other very closely; the inner margin, however, is much wider with *Eucypris* than *Cypricercus*. Additional difference is found in the muscle scar pattern.

Ecology.—Furtos found this form abundantly in Cold Spring Run, Ohio.

EUCYPRIS TUBERCULATA, n. sp.
Pl. 123, figs. 19,20

Side view.—Shell subtriangular, extremities equally rounded, shell higher than half its length; dorsal margin with slightly concave curvature, the highest point about two-fifths from the anterior end; shell densely covered with tubercle-like humps; inner margin about 0.24 mm. wide at anterior end, about 0.16 mm. at the posterior end; ventral margin nearly straight with small sinuation at the anterior third.

Dorsal view.—Shell compressed elliptical with bilateral symmetry.

Dimensions.—

Length	Height	H/L
1.19	0.70	0.59

Remarks.—Only one valve was found. The completeness and good preservation of the shell permits a complete description of this new species. A certain similarity was found with the genus *Cypricercus fuscatus* (Jurine).

Ecology.—Both *Eucypris* and *Cypricercus* are common forms in grassy ponds and swamps early in the season.

Genus LIMNOCYTHERE Brady 1867

LIMNOCYTHERE RETICULATA Sharpe
Pl. 123, figs. 21–23

Limnocythere reticulata Sharpe, 1897, p. 423–425, pl. 39, figs. 1–7. Hoff, 1942, p. 163–165, pl. 9, figs. 136–141.

Side view.—Shell subrectangular; dorsal margin straight ending with a small hump to anterior extremity; anterior margin broadly arched with a thin, wide, outer margin; posterior extremity similar to anterior but outer margin missing; ventral margin slightly sinuated in the center; surface deeply furrowed between three major humps; one dorsal and two ventral; the dorsal hump is located near one-third of length from posterior end, the one ventral hump at about half of the shell, the outer hump near the anterior end; anterior and posterior width nearly identical; shell slim and fragile; surface sculptured with fine reticules.

Dorsal view.—Arrow-shaped at the anterior end, trapezoidal and steeply falling off at posterior end.

Dimensions.—

Length	Height	H/L
0.64	0.29	0.45

Remarks.—There is only one shell in the collection. Hoff described dimensions of similar size. Staplin pictures a smaller and plumper looking form as *Limnocythere pseudoreticulata* (Staplin, 1954). The single valve in the author's collection does not permit comparisons on a larger scale.

Ecology.—Mostly found in running water, seldom in permanent lakes; Hoff (1942) describes it from temporary pools. It has a good tolerance to high currents as a bottom dweller.

Genus POTAMOCYPRIS
POTAMOCYPRIS PALLIDA Alm
Pl. 123, figs. 24–29

Potamocypris pallida Alm, 1914, Zool. Anz., v. 43, p. 470, fig. 2; Furtos, 1933, Ohio Biol. Surv., v. 5, p. 433, pl. 6, figs. 15–19.

Description of Right Valve

Side view.—Shell reniform, nearly of bilateral symmetry; anterior extremity more broadly curved than the posterior; dorsal margin evenly curved with a sharper bend anteriorly near the center of the shell; ventral margin nearly straight with a slight sinuation in the center portion. The inside view shows a wide inner margin at both extremities about one-seventh its total length. The muscle scars are characteristic for the genus *Potamocypris*. Shell smooth and translucent to transparent with widely scattered pore canals.

Dimensions.—

Length	Height	H/L	Width
0.69	0.38	0.55	0.18
0.58	0.33	0.57	
0.64	0.37	0.58	
0.66	0.37	0.56	
0.66	0.38	0.58	

Dorsal view.—Shell compressed elliptical with the anterior end pointed, the greatest thickness posteriorly behind the center steeply falling off to posterior end. Selvage section of the dorsal margin is recurved and accepts the center section of the dorsal margin of the left shell appearing like a groove.

Description of Left Valve

Side view.—Shell of trapezoidal outline, greatest height a little less than half the total length; extremities narrowly rounded, the anterior end more broadly rounded than the posterior end; dorsal margin broadly arched with stronger curvature near first third of length enclosing an obtuse angle to continue parallel with the posterior part of ventral margin; ventral margin straight to the center and continues straight again after break of about 30 degrees; shell smooth and transparent with a few scattered pore canals; muscle scars in the center and clearly visible with most specimens.

Inside view.—Inner margin approximately as wide as that of right valve, posterior end shows a thickened margin about half the width of the inner margin which enables a tight closure of the shell of the shorter right valve over the left valve.

Dorsal view.—Similar to right valve but shell appears to be flatter.

Dimensions.—

Length	Height	H/L	Width
0.65	0.35	0.54	0.15
0.65	0.32	0.49	
0.67	0.35	0.52	
0.62	0.31	0.50	
0.60	0.32	0.50	

THE STRATIGRAPHIC DISTRIBUTION OF THE OSTRACODES IN THE SILT

Occurrence	*Silt*			
	Base	*Middle*	*Top*	*Tufa*
Candona crogmaniana	3	2		
Candona decora	1			
Candona fossulensis	18			
Candona poseyensis	33			5
Candona scopulosa	55	29	63	18
Candona sigmoides				
Cypria nipissingae	9	1		1
Cypridopsis elongata	46	6	21	
? Cyprinotus sp.		2	4	
Eucypris pigra	3	2	2	
Eucypris rava	2			
Eucypris reticulata	1			
Limnocythere reticulata	1			
Potamocypris pallida	170	51	53	8
Total amount of valves	342	93	143	32

Remarks.—The species *Potamocypris pallida* Alm has two very different looking valves, the right with a much rounder dorsal margin than the left. The variation of the valve shape is little. The specimens correspond closely to the specimens of Furtos (1933).

Ecology.—Furtos (1933) found this species in cold and clear springs.

CONCLUSIONS AND SUMMARY

Seven ostracode genera and fourteen species are described from lake beds of Nipissing age about 4000 years before present. The fossiliferous lake silt is overlain by about fifteen feet of solid tufa rock of nearly the same age. *Candona scopulosa* is the most persistent form up into the tufa. About 80 percent of this species appears to be younger instars. The most common form near the base of the silt is *Potamocypris pallida.* Only a few ostracode species were found in the tufa rock. It is striking that half of the species are inhabitants of temporary ponds, although the lake was a large, deep, permanent lake with a probably shallow shore around the place where the silt was sampled. The lake bottom was probably muddy with only moderate vegetation. Most of the specimens were recovered from the lower part of the 5–10 inch silt layer; however, becoming smaller in number and size in higher horizons towards the tufa. The larger amount of specimens in the top layer is due to a larger size sample. Higher amount of lime apparently was available in the water while the higher silt horizons were deposited; this may be the reason for the progressive dwarfing of the forms.

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(*Explanation of* PLATE 123 *on next page.*)

EXPLANATION OF PLATE 123

FIGS. *1–3—Cypria nipissingae*, n. sp. *1*, left valve, side view, inside view; *2*, dorsal view; *3*, muscle scar pattern.

4–7—Cypridopsis elongata Kaufmann. *4*, right valve, side view; *5*, right valve, inside view; *6*, dorsal view; *7*, muscle scar pattern.

8–10—? Cyprinotus sp. *8*, left valve, side view; *9*, left valve, inside view; *10*, dorsal view.

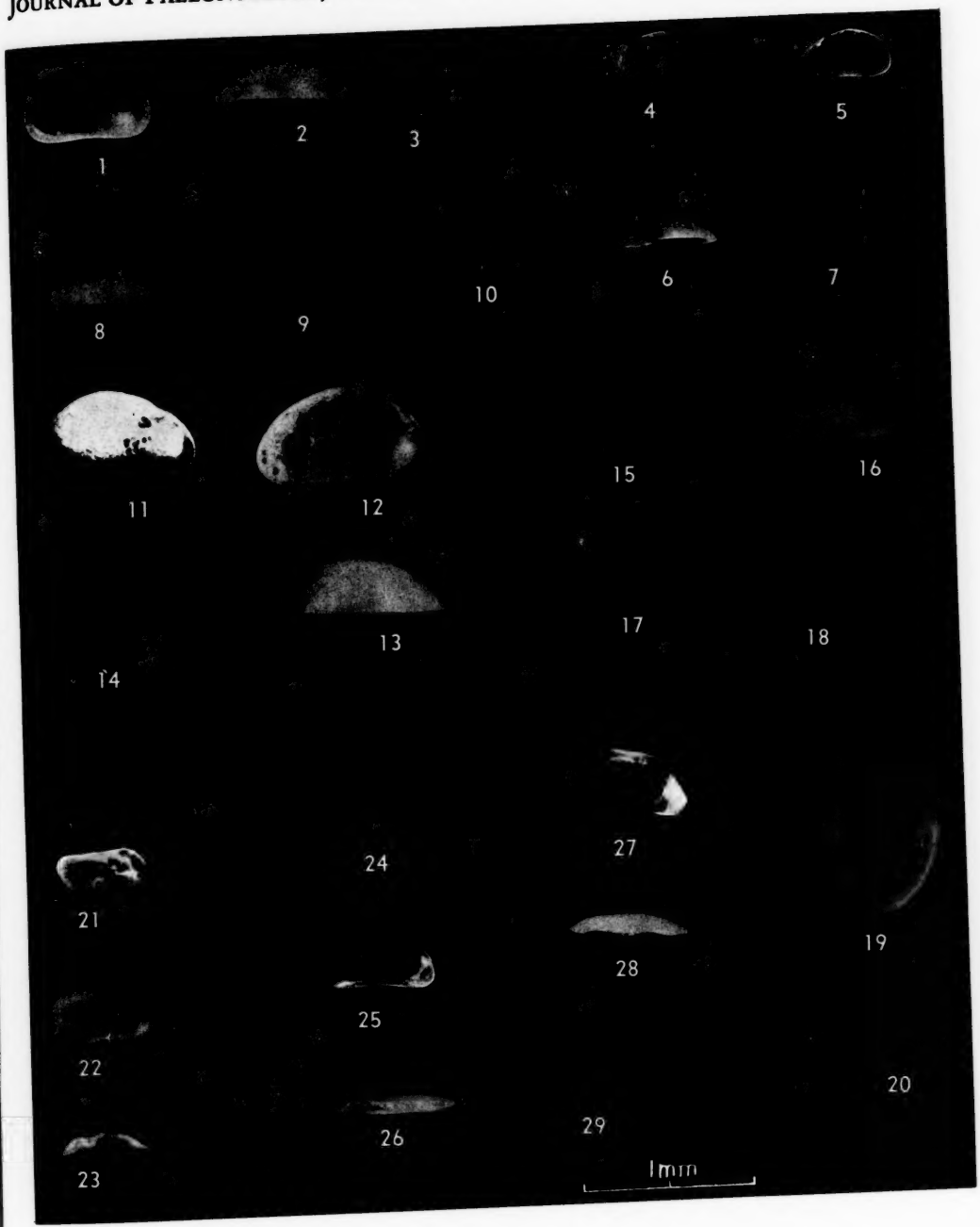
11–14—Eucypris pigra (Fischer). *11*, left valve, side view; *12*, left valve, inside view (infrared photo); *13*, dorsal view; *14*, muscle scar pattern.

15–18—Eucypris rava Furtos. *15*, left valve, side view; *16*, left valve, inside view; *17*, dorsal view; *18*, muscle scar pattern.

19–20—Eucypris tuberculata, n. sp. *19*, left valve, inside view (infrared photo); *20*, dorsal view.

21–23—Limnocythere recticulata Sharpe. *21*, right valve, side view; *22*, right valve, inside view (infrared photo); *23*, dorsal view.

24–29—Potamocypris pallida Alm. *24*, right valve, side view; *25*, right valve, inside view (infrared photo); *26*, right valve, dorsal view; *27*, left valve, side view (infrared photo); *28*, left valve, dorsal view; *29*, muscle scar pattern.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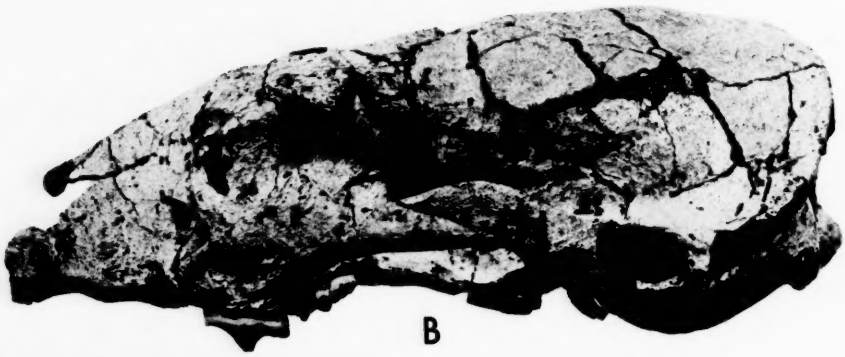

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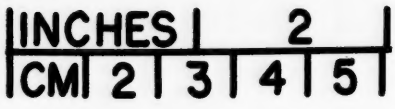

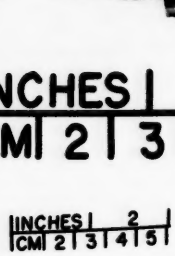

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A LATE PLEISTOCENE VERTEBRATE FAUNA FROM TEXAS

ARTHUR J. JELINEK

ABSTRACT—A Pleistocene fauna from the Foley gravel pits on a low terrace of the Wichita River near Wichita Falls, Texas is discussed and assigned to the time of the Wisconsin glaciation. The fauna includes: *Lepisosteus?* sp., *Cynomys ludovicianus* (Ord), *Geomys* cf. *bursarius* (Shaw), *Sylvilagus* cf. *audubonii* (Baird), *Taxidea taxus* (Schreber), *Mammuthus* sp., *Camelops hesternus* (Leidy), *Bison* (*Platycerobison*) *chaneyi* Cook, *Equus* cf. *leidyi* Hay. The fauna is similar to the Berclair terrace fauna of south central Texas and indicates a somewhat dryer climate than is now present in the Wichita Falls area.

INTRODUCTION

IN THE fall of 1953 and the spring of 1954 Dr. Walter W. Dalquest of the Midwestern University of Texas located and collected a number of fossil vertebrates from several gravel pits near Wichita Falls, Wichita County, Texas. The collection with which the present analysis is concerned was found in a group of pits owned by the Foley Sand and Gravel Company of Wichita Falls and located approximately seven miles northeast of that city on a terrace of the Wichita River. The author visited the locality in the late summer of 1955, at which time a vertical exposure of the section revealed between eight and nine feet of arenaceous red silt overlying an undetermined depth of water-laid sand and gravel. The contact zone at the top of the sand was cemented in many places, a condition not observed over one and a half feet below the contact. Fossil bone was observed and removed from the cemented zone of the sand at that time. Specimens recovered by Dalquest, and by Dalquest and Hibbard in April, 1954, all show evidence of cemented sand and gravel and are in a state of preservation similar to the bone recovered in 1955. A test for radioactivity conducted in 1958 at the University of Michigan Museum of Anthropology on (1) the 1955 sample from the top of the sand, (2) one of Dalquest's specimens, and (3) bone from the arenaceous silt, yielded the following results:

Sample (1 gm.)	Net alpha counts per minute
(1) 1955 sample from top of sand	$2.35 \pm .20$
(2) Bison bone collected by Dalquest in 1953	$2.47 \pm .21$
(3) *Cynomys* limb bones from arenaceous silt	$.15 \pm .25$

It is therefore assumed that the faunal assemblage was originally deposited near the top of the sand and below the base of the silt. The deposit is included in the Leona formation (Sellards *et al.*, 1932, p. 796), the sands presumably equating with part of the Wisconsin glaciation. The locality is here designated as the Foley gravel pits, and the fauna as the Foley fauna.

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EXPLANATION OF PLATE 124

FIGS. *A,B*—skull of *Taxidea taxus* (Schreber), *A*, ventral view; *B*, lateral view.
C—*Camelops hesternus* (Leidy), part of right lower jaw, M_2–M_3, lingual view.

the American Museum of Natural History for his interest and advice concerning the bison and horse material; Dr. T. M. Oelrich, of the University of Michigan Medical School, for his assistance and advice during the visit to the locality; and Dr. W. H. Burt of the University of Michigan Museum of Zoology and Mr. Karl F. Koopman of the Chicago Natural History Museum for permission to study specimens under their care.

CLASS PISCES (OSTEICHTHYES)
ORDER SEMINONTOIDEA
Family LEPIDOSTEIDAE
LEPIDOSTEUS? sp.

A single scale of a gar was recovered from the Foley gravel pits.

CLASS MAMMALIA
ORDER RODENTIA
Family SCURIDAE
CYNOMYS LUDOVICIANUS (Ord)

Cynomys ludovicianus (Ord), Hollister, 1916.

Two fossil skulls (UMMP nos. 31754, 31755) and several lower jaws of prairie dogs were found in the deposit. While both skulls are near the maximum size range of the blacktail prairie dog now in the area, neither exhibits sufficient size or dental variation with local recent specimens or affinities with other species or subspecies to merit different classification. The lower jaws were also, on the average, larger than those of the present population, but did not vary above its range.

Since a sample record of variation from a living prairie dog town nearby exhibited size differences significantly greater than those given by Hollister the results are presented here. The town is located two miles east of Harrold, Wilbarger County, Texas. The skulls of thirty-five individuals were studied. The measurements of these and the fossil lower jaws are given in the following table.

Family GEOMYIDAE
GEOMYS cf. BURSARIUS (Shaw)

Geomys bursarius (Shaw), Villa and Hall, 1947, Univ. Kans. Publ. Mus. Nat. Hist., v. I, no. 11, p. 229.

A right ramus containing P_4–M_2, a LP_4, and a left upper incisor (all UMMP no. 31756) are referred to this species. No characters are apparent which would distinguish them from the plains pocket gopher existing in the area at the present time.

TABLE 1—*Cynomys ludovicianus.*

Measurement (mm.)	Texas Specimens		UMMP 31754	UMMP 31755
	Range	Number		
Length; incisor to occipital condyles	57.9–64.2	18	—	—
Zygomatic breadth	41.5–46.9	18	—	—
Breadth posterior to maxillary-premaxillary suture	10.9–13.2	28	11.9	12.9
Breadth; post-orbital constriction	11.4–15.1	28	14.0	—
Breadth (maximum); maxillary	18.3–21.2	31	21.0	20.8
Breadth; outer borders of occipital condyles	13.6–15.7	20	—	—
Depth; occipital condyles	4.9– 6.2	20	—	—
Breadth; maxillary processes	18.3–21.7	31	21.7	20.6
Length; posterior border of incisive foramen to posterior border of palate	22.6–26.0	30	24.0	25.0
Length; palatal foramen to posterior border of incisive foramen, left side	15.4–18.7	30	17.5	17.8
Same, right side	15.6–18.8	31	17.4	18.0
Breadth; outer borders of tooth rows	18.5–22.8	22	21.2	20.4
Breadth; mesopterygoid fossa	3.7– 5.0	27	3.7	—
Depth; nasals to maxillary-premaxillary suture on diastemal palate	11.4–13.8	8	12.0	13.0
Length; P^3–M^3, left	16.4–18.6	32	18.4	17.8
Length; P^3–M^3, right	16.6–18.6	32	18.6	17.7
Length; incisive foramen, left	3.7– 5.8	30	4.5	3.8
Length; incisive foramen, right	3.6– 4.8	29	4.5	3.8

Anteroposterior length P_4–M_2	6.3 mm.
Anteroposterior diameter of P_4	3.2 mm.*
Transverse diameter of P_4	2.4 mm.
Anteroposterior diameter of incisor	2.7 mm.
Transverse diameter of incisor	2.5 mm.

* Taken on occlusal surface.

Order LAGOMORPHA
Family LEPORIDAE
SYLVILAGUS cf. AUDUBONII (Baird)

Sylvilagus audoboni Nelson, 1909.

A maxillary containing RP^2–M^3 and LP^2 of a small rabbit (UMMP no. 31757) is included in the fauna. It exhibits no characters which distinguish it from the desert cottontail found in the area at the present time.

Order CARNIVORA
Family MUSTELIDAE
TAXIDEA TAXUS (Schreber)
Pl. 124, figs. A,B

Taxidea taxus (Schreber), Hall, 1936. p. 77–83.
Taxidea taxus (Schreber), Miller and Kellogg.

A young adult badger is represented in the fauna by a partially complete skull, lacking a portion of the right zygomatic arch, the anterior border of the incisors, and all dentition except the left and right P^4 and M^1. The specimen exhibits some post-mortem lateral distortion and vertical compression. It is peculiar in several respects, although not sufficiently so to be classified as a distinct species. The features which vary most from badgers examined in the collections of the University of Michigan Museum of Zoology and the Chicago Natural History Museum are the relatively narrow zygomatic breadth, the comparatively heavy structure of the jugal in the sub-orbital region and a corresponding rugosity in the maxillary bone surrounding the infraorbital foraminae. A heavy cingulum of enamel is present on the lingual border of P^4. This feature appears to occur rarely, but at random in living badgers, and does not correlate with age, sex or geographic locality. The specimens in the two comparative collections which most closely match the Foley skull are young adult badgers from Cochise County, Arizona (UMMZ no. 77317) and Sonora, Mexico (CMMH no. 63899). A relatively complete set of measurements for the skull is compared below with those for the Michigan Museum specimen, followed by a comparison of the three specimens and the average measurements of twenty adult skulls of *T. taxus* from the Chicago Natural History Museum for zygomatic breadth, least depth of jugal and depth of occiput. From the series of skulls examined it appears that the zygomatic arch of the badger expands with full development of the temporal muscles following the eruption of the adult dentition. The Foley specimen and CNHM 63899 appear to have died following the full dental eruption, but prior to the maturation of the temporal muscles, and thus assumes a dolichocephalic aspect which does not have taxonomic significance.

Order PROBOSCIDEA
Family ELEPHANTIDAE
MAMMUTHUS sp.

The only evidence of mammoth recovered from the deposit other than fragments of limb bones is the basal fragment of a broken enamel tooth plate (UMMP no 31753). On the basis or relatively thin and closely folded enamel, as well as narrow width, it appears to be from a late species of *Mammuthus*.

Thickness of plate—14.0 mm.
Width of plate—60.0 mm.

Order ARTIODACTYLA
Family CAMELIDAE
CAMELOPS HESTERNUS (Leidy)
Pl. 124, fig. C

Auchenia hesterna Leidy, 1873.
Camelops hesternus Merriam, 1913.

A section of the right lower jaw of a large camel was found, containing M_2 and M_3 (UMMP no. 31749). The specimen is referred to *Camelops hesternus* on the basis of the convexity of the portion of the lower border of the jaw present. The comparatively flat faces between styles, the wider face behind the median style in both M_2 and M_3 and overall tooth dimensions. Tooth measurements are compared below with those given for *C. hesternus*, *C. huerfanensis* (Hay, 1921; Merriam, 1913), and *C. kansanus* (Hibbard, 1939).

TABLE 2—*Taxidea taxus*.

Measurement (mm.)	UMMP #31750	UMMZ #77317
Greatest length	117.6*	118.0
Greatest breadth at zygomatic arch	66.5*	76.3
Breadth across canines at alveolus	31.8	32.4
Least breadth between orbits	27.0*	27.1
Maximum breadth between post-orbital processes	34.3*	34.5
Least breadth of post-orbital constriction	28.8*	27.1
Least breadth between auditory bullae	12.7	13.3
Maximum length of bullae	26.9	27.7
Breadth at paroccipital processes	38.1	38.1
Least breadth between molars	15.8	18.3
Breadth at infraorbital foramenae	32.0*	31.6
Depth of occiput	35.0*	40.7
Length; anterior border of canine to posterior border of M^1	40.5	38.2
Alveolar length of P^3	4.8	4.4
Length of P^4	11.5	11.5
Breadth of P^4 (at right angle to outer surface)	10.0	10.0
Length of M^1 on interior face	11.4	10.8
Breadth of M^1	9.2	9.9
Length of canine at alveolus	8.4	7.9
Breadth of canine at alveolus	6.3	5.2
Breadth across mastoid processes	66.9*	72.0
Breadth across glenoid fossae	60.5*	66.4
Least depth of jugal in sub-orbital region	11.7	9.3

* Estimated correction for distortion included (±2 mm.).

Measurement (mm.)	UMMP #31750	UMMZ #77317	CNHM #63899	CNHM (20 skulls)
Zygomatic breadth	66.5±2.0	76.3	67.2	78.9
Depth of jugal under orbit	11.7	9.3	10.7	10.5
Depth of occiput	35.0±2.0	40.7	36.0	42.3

Family BOVIDAE

BISON (PLATYCEROBISON) CHANEYI Cook

Bison chaneyi Cook, 1928.
Bison (*Platycerobison*) *chaneyi* Cook, Skinner and Kaisen, 1947.

One horn core (UMMP no. 31752) of a large bison has been referred to *Bison* (*P.*) *chaneyi*. The only other bison material in the collection is a large thoracic vertebra (UMMP no. 31751) which is probably from an individual of the same species. The horn core is remarkable for its extreme curvature and posteriorly-twisted tip, as well as for a high degree of basal dorso-ventral flattening. It is separated from *Bison* (*Simobison*) *alleni* by much higher index of curvature in relation to index of compression (a trait which the specimen shares with the subgenus *Platycerobison*). In all measurements

TABLE 3—*Camelops*.

Measurement	*C. kansanus* KUMVP 4628	*C. huerfanensis* U.S.N.M. 8247	*C. hesternus* UCMP 20040	*C. hesternus* type	*C. hesternus* UMMP 31749
M_2, anteroposterior length	42.0	45.0	46.0	52.0	48.0
M_2, breadth	22.2	24.0	21.2	—	22.2
M_3, anteroposterior length	62.0	62.0	58.0	58.0	61.0
M_3, breadth	21.5	21.0	18.5	—	18.9

TEXT-FIG. 1—*Equus* cf. *leidyi* Hay, LP_3–M_3, occlusal view, ×1.

the horn core closely parallels and is somewhat larger than *Bison* (*Platycerobison*) *geisti* described from Alaska. In view of the size of the Foley specimen, the fact that it was found in a depositional situation similar to *Bison chaneyi*, and the lack of knowledge of the size range of *B. chaneyi*, the horn core is assigned to this species.

The late Pleistocene age of *Bison* (*Platycerobison*) *chaneyi* and other species of the subgenus tends to strengthen Skinner and Kaisen's postulated affinities of *B. chaneyi* with Old World *B. priscus* as well as their hypothesis of retrogression in horn core size. The morphologically older form (*B. chaneyi*) would tend to be found at the extremes of distribution and the more evolved retrogressive forms (*B. geisti*) nearer the distribution center. Comparative measurements of the holotypes of *B.* (*P.*) *chaneyi*, *B.* (*P.*) *geisti*, and the Foley horn core are as follows:

TABLE 4—*Bison* (*Platycerobison*).

Measurements (in mm.)	*B.* (*P.*) *geisti* U.A.-F: AM 46894	*B.* (*P.*) *chaneyi*	
		UMMP 31752	CMNH 1147 Holotype
Horn core length on upper curve	360	410	545
Horn core length on lower curve	425	535	630
Length, tip of horn core to upper base	280	295	440
Transverse diameter of horn core	121	127	147
Vertical diameter of horn core	88	96	114
Circumference of horn core at base	340	355	412
Index of curvature	152	181	143
Index of compression	73	75	78
Index of proportion	106	115	132

Order PERISSODACTYLA
Family EQUIDAE
EQUUS cf. LEIDYI Hay
Text-fig. 1

Equus leidyi Hay, 1913.

Equidae are represented in the Foley fauna by a portion of the left lower jaw of a medium-sized horse, which contains five teeth P_3-M_3 (UMMP no 31748). On the basis of tooth size and enamel pattern the specimen has been referred to *Equus* cf. *leidyi* Hay. The teeth are somewhat smaller than most examples of *E. complicatus*, and in almost all respects are similar to specimens referred to *E. leidyi*. In particular they compare favorably in size with Hay's (1917) measurements of refered specimens of *Equus leidyi*. The enamel pattern is characterized by a lack of excessive plication. The hypolophid bears a distinct pli caballinid fold in both molars and premolars, and is advanced into the valley between the entoflexid and metaflexid in the molars. The metaconid and metastylid retain a constant pattern in molars and premolars; the former, relatively narrow and curving, terminates in a sharp anterior fold; the latter exhibits a wide posterior flare and also terminates in a sharp anterior fold. The intervening valley is headed by a distinct V in the molars, is rounded in the pre-molars, and is most constricted at its mouth by the anterior flexure of the metaconid in M_2 and M_3. The enamel pattern closely matches specimens of both *E. complicatus* (Sellards, 1915, fig. 43, specimen no. 1752 referred to this species by Hay, 1929; Hay, 1914, figs. 53,61,64, pl. xi., fig. 2; Hay, 1917, Pl. II, fig. 1) and *E. leidyi* (Simpson, 1930, p. 584, Hay 1917, Pl. II). On the basis of general resemblance in tooth size to *E. leidyi* rather than *E. complicatus*, especially as concerns the dimensions of M_3, the specimen is tentatively assigned to the former species.

The following table of tooth measurements is given to compare the size of enamel occlusal surfaces of the Foley specimen with referred specimens of *E. leidyi* and *E. complicatus*.

DISCUSSION

The presence in the Foley fauna of forms of known ecological affinities, such as the blacktailed prairie dog, the desert cottontail, and the plains pocket gopher, suggests a climate at the time of the formation of the deposit similar to that in the area at the present time. The fact that the present center of distribution of these forms lies to the west of the area in which the fossils were collected indicates that the Foley fauna existed in a somewhat dryer climate, approximating that of the southwestern Great Plains. Closest affinities of the fauna appear to be with the Berclair terrace fauna from Bee County, Texas (Sellards, 1940), where *Equus leidyi* was found in association with

TABLE 5—*Equus*.

Measurement (in mm.)	*E. leidyi*		USNM 4086	*E. complicatus*		USNM 705–707
	UMMP 31748	Hay, 1917		Hay, 1917	SUI 219	
P_3 anteroposterior length	27.4	28.5	—	30	31	34
breadth	15.9	16.5	—	17	18	18
P_4 anteroposterior length	26.9	27	—	29	30	31.5
breadth	16.2	15	—	17	20.5	18
M_1 anteroposterior length	24.5	25	—	25.5	28	28
breadth	15.5	13	—	15	18	16
M_2 anteroposterior length	25.1	29	—	—	28	28
breadth	14.9	15	—	—	16.5	16
M_3 anteroposterior length	29.8	30	30	—	37	—
breadth	12.8	12.5	11	—	14	—

Mammuthus columbi and unidentified species of *Camelops* and *Bison*. All other forms are essentially similar to the present fauna. The nature of the deposit substantiates the late Pleistocene affinities of the Foley fauna, which is here assigned a Wisconsin age.

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A REVIEW OF THE OLIGOCENE INSECTIVORE *MICROPTERNODUS BOREALIS**

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ABSTRACT—A rostrum from the Chadronian of Pipestone Springs, Montana is referred to *Micropternodus borealis* Matthew. *Kentrogomphios strophensis* White is a junior synonym of *M. borealis*, as may be the *Cryptoryctes kayi* Reed humeri. *Micropternodus* cannot be placed in the Talpidae, Solenodontidae, Apternodontidae, or the Nyctitheriidae, as has been variously suggested by previous authors, but rather belongs in a poorly-known complex of late Cretaceous and early Tertiary insectivores represented by *Gypsonictops*, *Scenopagus*, and the Geolabidinae.

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BEFORE Dr. J. LeRoy Kay retired as the curator of vertebrate paleontology at the Carnegie Museum, he sent to Dr. M. C. McKenna a rostrum and ten jaw fragments provisionally identified as *Micropternodus* which were generously turned over to me for study. I am very grateful to Dr. McKenna for his patient guidance and many helpful suggestions. I would also like to express my appreciation to William A. Clemens, John E. Mawby and S. David Webb who aided greatly in the crystallization of my conclusions. Mr. Owen J. Poe has prepared the illustrations.

PREVIOUS STUDIES

In 1903 W. D. Matthew described *Micropternodus borealis* from a lower jaw and incomplete dentition collected near Pipestone Springs in southwestern Montana. His type contains P_3–M_3 and the alveoli for the anterior teeth. Matthew placed his new genus within the Zalambdodonta (in which he included the Chrysochloridae, Tenrecidae, Solenodontidae, *Potamogale*, and *Necrolestes*) stating that, although it was not too different from living zalambdodonts, it had no close extant relatives. He wrote later, in 1919 (p. 174) that *Micropternodus* may possibly be distantly related to *Solenodon*.

E. M. Schlaikjer (1933, p. 20) listed the following similarities between *Micropternodus* and *Solenodon:* "dental formula $\frac{3-1-3-3}{}$; I_2 larger than either I_1 or I_3; P_2 two rooted; antero-posterior ridge on talonid confluent with base of trigonid; general shape of the mandible; position of anterior base of coronoid process." He thus considered *Micropternodus* closely related and possibly ancestral to *Solenodon* and placed it within the Solenodontidae. *Apternodus* was included in the same family as the type of a separate, closely related subfamily, probably derived from a Paleocene insectivore similar to *Palaeoryctes*.

In their classic revision of the mammalian fauna of the White River Oligocene, Scott and Jepson re-illustrated *Micropternodus borealis*, republished Matthew's original description, and referred it, with doubt, to the Solenodontidae. Also referred, presumably with the same doubt, was *Clinopternodus gracilis* Clark, which they considered to resemble *Micropternodus* in crown structure. They observed, however, that the lower teeth of *Clinopternodus* were more anteriorly inclined, more closely compressed, and about one-third larger than those of the latter genus. The type is an anterior fragment of a mandible containing C_1, P_3, P_4, M_1, and the alveolus for P_2. Clark (1937, p. 309) added that the teeth were more incurving than those of *Micropternodus*, and was dubious about P_2 being double-rooted, thinking it not likely.

In his study of the Canyon Ferry vertebrate faunules, Theodore E. White (1954) described the skull and right lower jaw of an enigmatic insectivore which exhibited puzzling characters definitely excluding it from the coricids on the one hand and seeming to ally it with bats on the other. He noted its talpid-like adaptations but referred the genus to Simpson's Nyctitheriidae because

* A contribution from the University of California Museum of Paleontology.

its uniqueness prevented its assignment to a better known or more clearly defined group. As will be seen below, White's *Kentrogomphios strophensis* is actually the previously unknown skull or *Micropternodus borealis*.

Jean Hough (1956, pl. 62, figs. 16 and 17) figured two lower jaw fragments in a preliminary report of the Cameron Spring faunule* (in which she discussed the status of the Tenrecoidea and described *Oligoryctes cameronensis*), which she has called *Micropternodus* sp. McKenna (in press) has stated that the mandible shown in pl. 62, fig. 17 is clearly referable instead to *Geolabis* (= *Metacodon*) although on the basis of new material from Pipestone Springs, it seems likely that the other specimen (fig. 16) is indeed *Micropternodus*. Hough concludes that *Micropternodus* and *Clinopternodus* should be separated from the solenodontids and be allied to Matthew's Apternodontidae, which she revives.

Samuel B. McDowell, Jr. (1958, p. 175) refuted Schlaikjer's arguments for placing *Micropternodus* in the Solenodontidae. He believes that no one of the characters listed by Schlaikjer is sufficiently unusual to be real evidence of relationship and correctly predicted, upon examination of the position and form of the hypoconids, that the upper dentition of *Micropternodus* would be dilambdodont. Furthermore, because of the fact that what was then known of *Micropternodus* and *Clinopternodus* showed no particular resemblence to *Solenodon*, he followed Hough by removing these genera from the Solenodontidae and placed them insead in the Nyctitheriidae.

Most recently John Clark (personal communication to McKenna) has noticed the similarity between *Kentrogomphios* and the Garnegie Museum skull from the type locality of *Micropternodus* and correctly suggested that the two genera are synonymous. McKenna states (in press) that the Carnegie Museum skull does not exhibit any close affinity to *Solenodon* other than that both are lipotyphlan insectivores.

* "... a mile NE of Cameron Spring, Wyoming, Center W line SE¼W¼ sec. 1, T32N. R90W, Fremont County, Wyoming." The faunule is considered to be Chadronian (early Oligocene) in age.

DESCRIPTION

Micropternodus borealis Matthew, 1903.

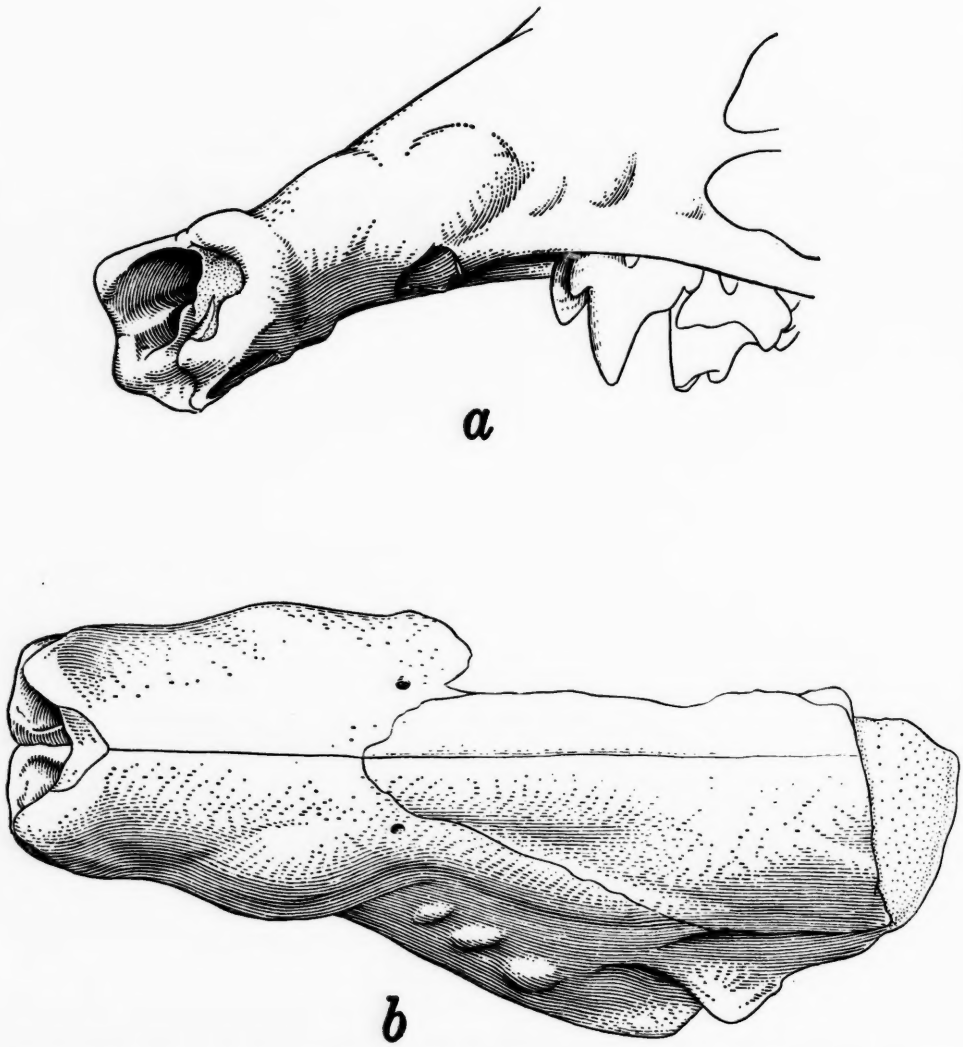
Kentrogomphios strophensis White, 1954, pp. 404–407.

Holotype.—A.M.N.H. No. 9602, left lower jaw with P_3–M_3 and alveoli of the anterior teeth.

Distribution.—Chadronian, Oligocene, Montana and Wyoming, type locality: Pipestone Springs, Montana.

Referred Material.—C.M. no. 8674, anterior skull fragment; C.M. nos. 8675, 8676, 8677, 8678, 8679, 8898, 9219, 9267, 8896, 9897, lower jaw fragments; main pocket, Pipestone Springs, Montana. U.S.N.M. no. 18870, anterior skull fragment; U.S.N.M. no. 18871, lower jaw fragment; loc. no. 24LC16, Canyon Ferry, Montana. Specimen shown in fig. 16, pl. 62 of Hough (1956), Cameron Spring, Wyoming (no specimen number given).

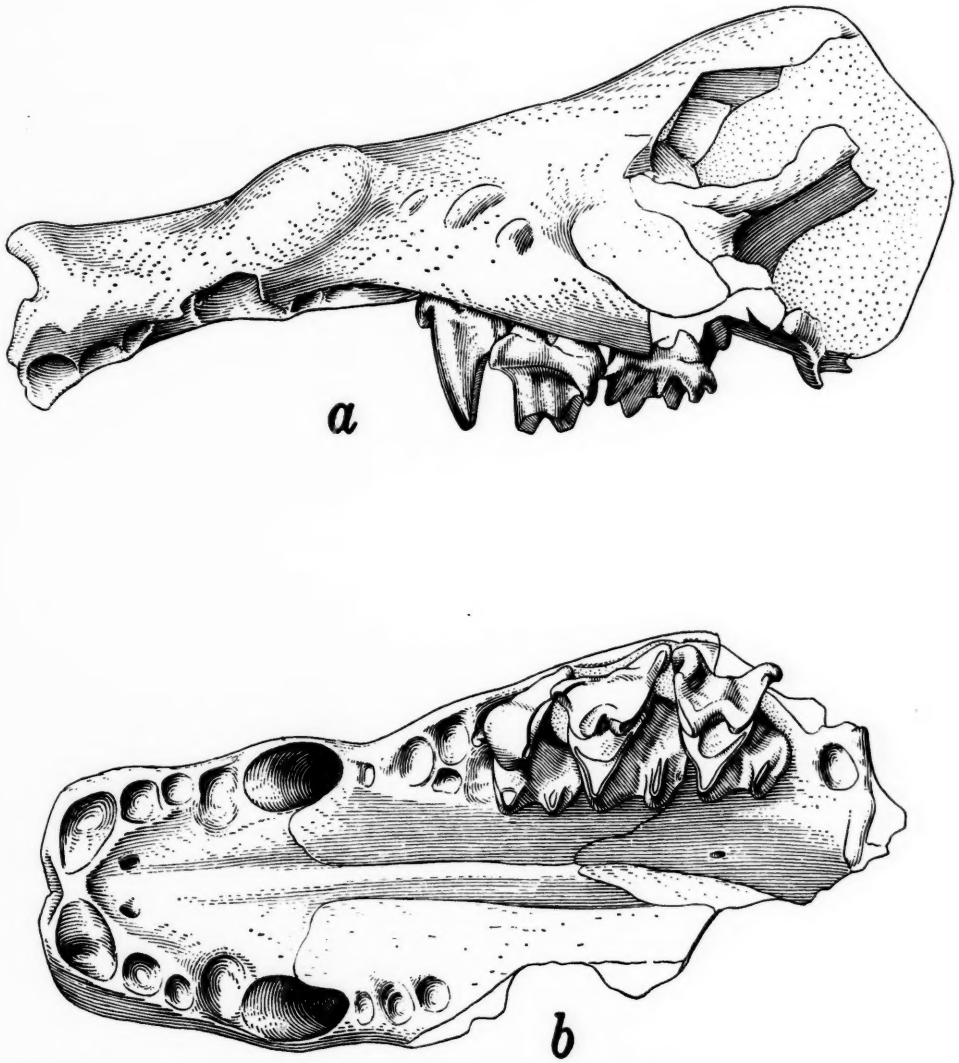
Skull. The referred skull fragment from Pipestone Springs is the well-preserved rostrum of an insectivore approximately the same size as *Talpa europaea*. The snout is elongate and broad. Its ventral surface bears the left P^4–M^3 and the alveoli for I^1–P^3 on both sides. Two unique projections (see illustrations) extend over the external nares, partially encapsulating them, much in the same manner as in *Chrysochloris*, but more dorsomedially placed. They presumably housed an enlarged tactile organ. The sutures of the skull are fused, making description of individual bones practically impossible. There are, however, indications of a suture passing down the midline of the skull and very vague signs of another that may have outlined the anterior portions of the frontals. There is a large, bulbous expansion on either side of the skull which enclosed the enlarged root of the canine. Posterior to these are small lateral swellings marking the posterobuccal root of P^3 and two somewhat larger ones for the buccal roots of P^4. Between the dorsal apices of the canine roots are two diminutive foramina which may have served to transmit blood vessels to the muscles on the dorsal surface of the snout. The infraorbital foramen is short and large, with a deep oval pit in front of its anterior aperture. White believes a slender zygomatic arch was present



TEXT-FIG. *1*—*A*, C.M. no. 8674, *Micropternodus borealis* Matthew, anterolateral view of the left side of the rostrum, ×5; *B*, C.M. no. 8674, *Micropternodus borealis* Matthew, dorsal view of rostrum, ×5.

and indicates a large lacrimal duct within the orbit. No lacrimal tubercle is apparent on either the Carnegie Museum or the Canyon Ferry skull. The incisive foramina are small and are situated between I^1 and I^2 on the extreme anterior surface of the palate, as in the Talpinae. The anterior opening of the palatine canal is present on the right side of the skull halfway between the protocone of M^2 and the midline of the skull. A tiny groove extends anterior to it, running parallel to the midline of the skull as far forward as a position medial to P^3.

On the dorsal surface of the snout there are faint depressions and grooves, presumably once areas of muscle attachment in the living animal. A long, flat, triangular depression on the rostrum dorsal to the ante-



TEXT-FIG. *2*—*A*, C.M. no. 8674, *Micropternodus borealis* Matthew, lateral view of the left side of the rostrum, ×5; *B*, C.M. no. 8674, *Micropternodus borealis* Matthew, ventral view of the rostrum, ×5.

rior opening of the infraorbital canal probably served as the origin of the M. levator labii superioris proprius as in *Solenodon* (see Dobson, 1882, pl. 9, fig. 11). The anterior border of the canine alveolus may have served for the origin of a muscle homologous to the unnamed one located ventral to the anterior tendon of the former muscle, as is the case in *Desmana* (see Dobson, 1882, pl. 18, fig. 1). Posteriorly and slightly above the M. levator labii superioris proprius is a shallow groove which may have served for the origin of the M. fronto-cuticularis.

Upper dentition. Dental formula: I_3^3, C_1^1, P_3^3, $M_3^3 \times 2 = 40$. Unfortunately, only the alveoli of the teeth anterior to P^4 are preserved in the Pipestone Springs skull. The alveolus for I^1 is transversely elongate and

indicates that this tooth was enlarged, flattened and medially directed, probably very much resembling the condition in *Talpa europaea*. The alveoli for I^2 and I^3 are closely appressed and progressively smaller than I^1; I^2 about three-fourths the diameter of I^1; I^3 about one-half the diameter of I^1. Immediately posterior to I^3 is a large oval pit on the alveolar border which received the apex of the lower canine. As mentioned above, the alveolus of the upper canine is greatly enlarged, indicating a large "saber-tooth." In the Pipestone Springs skull it is elliptical in shape, narrowing somewhat posteriorly. In White's illustration of the Canyon Ferry specimen the canine alveolus is much more compressed and shows an invagination on the posterior lingual border that is not so well developed on the Pipestone Springs skull.

P^1 is assumed to be absent. There is a very slight diastema on each side of the minute, single-rooted P^2. Only the alveoli for the three roots of P^3 remain in the Pipestone Springs skull, but the illustration of the Canyon Ferry specimen shows the tooth to have a high paracone and a long, trenchant ridge extending up the posterolabial side, giving the impression that the tooth had been diagonally implanted. In White's illustration the left P^3 has a well-developed protocone although the same tooth on the opposite side has only a slight cingulum representing the protocone. The P^4 is submolariform, larger than P^3, and has a similar trenchant ridge running from the paracone to a cusp in the position of a metastyle of the molars, paralleling the same structure in P^3. The paracone is higher and the stylar cusps are more heavily developed than in P^3. There is a peculiar hook-like cusp on the anterior base of paracone. The metastyle is placed directly dorsal to the parastyle of the M^1 in the Carnegie Museum skull, although White's skull does not show this. The protocone is large, having nearly half the height of the paracone. The hypocone is also well developed and is located on a broad shelf extending posteriorly from the base of the protocone to a position just past the midline of the tooth, forming a bowl-like excavation in the posterior side of the tooth. There is a cingulum posterior to the hypocone.

M^1 is not as high crowned as P^4. The protocone is broad and "V"-shaped, opening labially, and is unconnected by crests to the apices of either the paracone or the metacone. It is a little higher than that of P^4. The paracone and metacone are close together and form a portion of a shearing edge which projects posterobuccally to include the metastyle. The metastyle bears a short, bud-like fork posteriorly and is connected anteriorly to the smaller parastyle by a buccal cingulum. There is a strongly-developed hypocone having a transverse ridge and a posterior cingulum. The hypoconal shelf extends three-quarters of the way to the buccal edge of the tooth.

In contrast to M^1, M^2 exhibits a striking dilambdodont pattern, with a distinctly separate metacone and paracone, and has a bizarre doubly-tined parastyle (see "*Metacodon*" = *Geolabis*, Patterson and McGrew, 1937, p. 259). A mesostyle is present. The metastyle is also doubly-tined and completes the posterior end of a deep-valleyed, "W"-shaped ectoloph. The protocone is similar to that of M^1. The hypocone is grossly like that of the preceding tooth, but is heavier and the buccally directed ridge bends slightly posteriorly. This is the reverse of the case in the Canyon Ferry specimen, in which it curves anteriorly towards the side of the protocone. The hypoconal shelf is bulkier and more abbreviated than in M^1.

The M^3 is lost from the Pipestone Springs skull but is retained in the Canyon Ferry rostrum and will be described from White's illustration. The trigonid of the tooth is much reduced and more cuspate when compared with the other molars. The anterior half of the dilambdodont ectoloph pattern is present with its greatly enlarged parastyle (with a parastyle, see White, p. 404) and a mesostyle. The metastyle is absent and the tooth lacks the hypoconal shelf entirely. There are alveoli for three roots along the tooth's posterior margin.

Lower jaw. In addition to Matthew's excellent type specimen, A.M.N.H. no. 9602, there are ten new jaw fragments from the type locality of *Micropternodus borealis*. The horizontal ramus of the lower jaw is long and slender with a slightly concave lower border. Hough (1956, p. 537) was in error in stating that the lower border was straight. Its concave nature is partly shown in pl. 62, fig. 16

in that paper. The symphysis is long and extends ventroposteriorly, making a slightly rounded swelling in the profile of the jaw beneath P_3 (see Matthew, 1903, fig. 3). A single mental foramen is placed ventral and somewhat anterior to P^3 on the buccal face of the jaw. There is a shallow groove running antero-posteriorly just below the midline on the opposite (lingual) side of the horizontal ramus.

The ascending ramus of the mandible rises steeply from a wide "T"-shaped (in cross section) base close behind m_3. The mandibular condyle is low, on a level with the biting surface of the teeth. The masseteric fossa is deep and distinctly marked. Hough's photograph (1956, pl. 62, fig. 16) shows the coronoid process to be high and triangular, resembling that of *Microgale*. There are indications that a small, slender angular process existed on the gently curved lower margin of the ascending ramus.

Lower dentition. Matthew (1903, p. 205) originally described the anterior lower dentition as follows: "P_2 small and one-rooted, canine small, incisors small, subequal." Schlaikjer (1933, p. 20) expanded this description by adding that the alveolus for I_2 was larger than those for I_1 or I_3. It has also been noted that the medial pair of incisors is correspondingly enlarged in the upper dentition. He said further that the lower canine alveolus is larger than any one of the incisors, a fact borne out by a depression just anterior to the upper canine. Schlaikjer also found that Matthew's "slight diastema behind P_2" is actually the locus of the posterior root of P_2. McDowell (1958, p. 175) considered that it was equally likely that these alveoli contained the separate roots of a single-rooted P_1 and P_2. However, it is seen that the upper dentition lacks a P^1 and occlusal relationships suggest that Schaikjer was correct.

P_3 is two-rooted, has a slightly recurving protoconid, and possesses a well-developed posterior heel, which descends rapidly as it approaches the buccal side of the jaw. A wear surface shows on the posterolingual slope of the protoconid and there is a nubbin in the position of a paraconid low on the crown of this cusp. The metaconid is absent.

The protoconid is higher and more recurving in P_4 than in the preceding tooth. The heel is somewhat heavier and better-developed but still lacks cusps. The paraconid is higher than on P_3, being nearly one-half as high as the protoconid, sends a short ridge anterolabially, and is connected to the base of the metaconid by a short lingual cingulum. The metaconid is well-developed on this tooth.

The protoconid is the dominant cusp of the trigonid of M_1 and makes it the highest crowned tooth in the lower jaw. The metaconid lies directly lingual to it and is broadly connected to the protoconid. The paraconid is situated on the anterolingual side of the tooth and is separated from the metaconid by a shallow valley. It is two-thirds as high as the protoconid and is connected to it by a lingual ridge. An anterior cingulum descends steeply from the paraconid to a point on the anterobuccal base of the protoconid. The talonid is as long as the trigonid and about half as high as the protoconid. The hypoconid is distinct, "V"-shaped, and is connected by a crest to a point near the center of the posterior wall of the trigonid. An entoconid and hypoconulid are connected with the hypoconid by a sharp posterior ridge and all are separated from the trigonid by a deep rounded valley.

M_2 is essentially like M_1, except that the paraconid is larger and more lingually placed, the posterior crest on the talonid is shortened, and the tooth is slightly lower crowned than M_1.

On M_3 the height of crown is further lessened, the hypoconulid is lost, and the hypoconid is connected to the metaconid by a crest. Otherwise it closely resembles the other molars. These last two molars are indistinguishable from those of U.S.N.M. no. 18871, the referred jaw of *Kentrogomphios strophensis*.

DISCUSSION

There is no question that the newly collected insectivore mandibles from Pipestone Springs, the type locality of *Micropternodus borealis*, do belong to that species. It then remains to be established whether or not the strange new rostrum discovered there is a portion of the formerly unrecognized skull of *Micropternodus*. The length of the cheek tooth row is the same in the upper and lower dentitions, and the relative height of crown

is highest in the center of the rows between P^4 and M_1. In the lower jaw the alveoli for the incisors show than I_2 is the largest of these teeth, while I^1 is the largest of the upper incisors (making a very neat nipping device notably similar to that of the Talpinae). One of the more complete lower jaws was occluded with the upper teeth and it was found that the dentitions fitted one another perfectly. Because of the peculiar configuration of the crowns of the upper teeth and their high-cuspate nature, it seems unlikely that any known inferior dentition could interlock better than that of *Micropternodus borealis* and, because of the circumstances that both elements were collected at the same locality and that White described a similar pair of upper and lower jaws in sediments of Chadronian age near Canyon Ferry Reservoir, it is here concluded that the jaws and rostra from Pipestone Springs belong to *Micropternodus borealis*.

The following differences have been noted while comparing White's illustration and description of *Kentrogomphios* with the *Micropternodus* skull from Pipestone Springs:

1. The hypoconal ridge of M^2 is directed anterolabially in *Kentrogomphios strophensis*. In *Micropternodus borealis* it parallels the posterior edge of the trigonid.
2. The alveolus for the upper canine in *M. borealis* is more distinct on the surface of the rostrum, and is less laterally compressed than in *K. strophensis*.
3. A line drawn through the gum line from P^4 to M^3 meets a line similarly drawn from I^1 to P^3 at an angle of 30° in *M. borealis*, while the alveolar border of *K. strophensis* is essentially straight.

The differences of the hypoconal ridge on the M^2 between the two skulls may be minimized upon considering the great differences in the development of the protocone of the right and left P^3 shown on the Canyon Ferry skull. White mentions that the preservation was poor at the type locality of *Kentrogomphios strophensis*, which may in part, at least, account for the dissimilarity of the canine alveoli and the alveolar border of the two specimens. The jaw material of *Kentrogomphios strophensis* is indistinguishable from that of *Micropternodus borealis*. Then, on the basis of the otherwise virtual identity of the dentitions, and in the absence of definite knowledge of variation in the form, it is believed that *Kentrogomphios strophensis* is best considered a junior synonym of *Micropternodus borealis*. Both specimens have been collected from localities of Chadronian age which are separated by a distance of only 40 miles.

Three humeri were included in the faunal list described by White from his "*Kentrogomphios*" locality, one of which Reed (1956, p. 310) examined and concluded belonged to *Cryptoryctes*. Reed further mentioned the interesting possibility that this humerus may belong to "*Kentrogomphios*." He listed (1954a, p. 107) some skull/humerus ratios of recent fossorial to semi-fossorial insectivores: *Scapanus* 229%, *Condylura* 245%, *Sorex* 248%, *Neurotrichus* 304%. In an attempt to allocate *Cryptoryctes* and *Arctoryctes* either to the possibly fossorial epoicotheriid edentates (*Epoicotherium* and *Xenocranium* respectively) or the Apternodontinae, Reed used these ratios as evidence to suggest that the humeri represented animals that might have fitted into either of these two groups. If one assumes that *Micropternodus* had a skull roughly of the same proportions as that of *Talpa*, then the length of its skull can be estimated at 27 mm. Further, assuming this tentative figure is approximately correct, the following ratio is obtained:

$$\frac{\text{estimated skull length of } \textit{Micropternodus}}{\text{length of type } \textit{Cryptoryctes kayi} \text{ humerus}} = \frac{27 \text{ mm.}}{10.9 \text{ mm.}} = 248\%$$

This is much closer to the skull/humerus ratios of the above insectivores than those obtained from epoicotheriid (306%) or apternodontin (424%) skulls. Little more can be added at present to substantiate the supposition that the *Cryptoryctes* humeri may be skeletal elements of *Micropternodus* other than the circumstantial evidence that *Cryptoryctes* humeri are recorded from both of the better-known *Micropternodus*-containing faunas.

RELATIONSHIPS

Micropternodus has already been classified (1) loosely within the Zalambdodonta by Matthew—a taxonomic grouping generally considered at present to be invalid; (2) by Schlaikjer more specifically into the Solenodontidae along with *Apternodus;* (3) with *Clinopternodus* doubtfully in the Solenodontidae by Scott and Jepson; (4) by White and later McDowell in the Nyctitheriidae for want of a better allocation (McKenna, in press, believes this family is invalid); and finally (5) by Hough in Matthew's revived Apternodontidae.

In spite of its mole-like adaptations, such as a long, flattened snout with its peculiar anterior protuberances and the dilambdodont pattern common in moles, I do not believe that *Micropternodus* is very closely related to the talpids. The character and position of its hypocone, the distinct cusps of the upper molars and the subdivided stylar cusps exclude it from any moles known to me.

The upper dentition does not resemble that of *Solenodon* and thus supports McDowell's thesis for removing the genus from the Solenodontidae. The snout is much more tubular in *Solenodon*, the canine is much smaller, and I^1 is greatly enlarged and projects somewhat posteriorly from a ventral extension of the premaxilla. *Nesophontes* resembles *Micropternodus* in that the canine is is enlarged, the upper molars are dilambdodont, and the snout is broad. However details in the construction of the anteriormost portion of the rostrum differ greatly, the incisive foramina are much larger in *Nesophontes*, the molars show no detailed resemblance and the hypocone is represented only by a small posterior cingulum in the latter form. It is not surprising that *Micropternodus* is so unlike the endemic Antillean insectivores considering that it is so widely separated from them geographically and especially in time.

Because the definative characters of Simpson's Nyctitheriidae are so generalized, it would indeed be possible to include *Micropternodus* in this family. But *Micropternodus* is a uniquely specialized mammal and does not especially resemble any of the genera usually placed there. McKenna (in press) has separated from the Nyctitheriidae several closely related forms, including some former species of *Nyctitherium* which he believes belong to another genus, and has resurrected the Amphilemuridae for their reception. *Micropternodus* is not referable to the Amphilemuridae because it has high trigonids, the P_2 and P_3 are double-rooted, and P_3 and P_4 are subequal in height.

Hough (1956, p. 541) considered that *Micropternodus* was a variant derived in pre-Oligocene time from a common stock with *Apternodus*. This certainly may be true, but the relationship must be a rather remote one since *Apternodus* differs so radically from *Micropternodus* in its heavily constructed skull and jaws, the greatly enlarged medial upper and lower incisors, the blunt, double-rooted canine, and the simplified, zalambdodont upper molars. The hypoconal development is at a minimum and the rostrum is totally different from that of *Micropternodus*. There is little reason for holding these two very different insectivores in the same family.

The rostrum of *Geolabis* (McKenna, in press) does not resemble that of *Micropternodus* greatly. The tubular shape of the rostrum is dissimilar to the condition in *Micropternodus* and the infraorbital is much longer in the former genus. Dentally, however, resemblance can be seen in the general arrangement of the upper and lower molar cusps, the "V"-shaped protoconal shelves, and in the high development in the stylar areas. Both forms have a secondary cuspule on several of the stylar cusps, thus giving a forked appearance to the me^s M^1, me^s, pa^s M^2, pa^s M^3 of *Micropternodus* and the pa^s M^1, pa^s M^2, pa^s M^3 of *Geolabis*. It seems to me that the geolabidines and *Micropternodus* represent separate phyla of a poorly-known radiation of early Tertiary insectivores.

The upper dentition of *Scenopagus mcgrewi* McKenna and Simpson (1959) from the Bridgerian of western Wyoming may be that of a comparatively unspecialized relative of *Micropternodus* and the geolabidines. The protocones of the molars of *Scenopagus* are "V"-shaped and oriented as in *Micropternodus* and *Geolabis* and the configuration of the cusps of the cheek teeth is also close to

these Oligocene insectivores, although the cheek teeth are somewhat more bunodont in *Scenopagus*. Stylar development is, however, weak and the hypoconal shelves are not nearly as large as those in *Micropternodus*. The infraorbital foramen of *Scenopagus* is longer than that of *Micropternodus* and in this respect resembles *Geolabis* more closely.

As suggested by Simpson (1951) the synthetic "dentition" of *Gypsonictops* of the Cretaceous Lance Formation resembles "*Metacodon*" (=*Geolabis*) and the genus might be considered as an ancestral geolabidine (see McKenna on the Geolabidinae, in press). While remaining aware of this vast temporal gap, the following similarities between *Gypsonictops* and *Micropternodus* may be noted. In the lower molars both genera exhibit relatively high trigonids with low talonids, an anterior cingulum that runs steeply upward from the base of the protoconid towards the apex of the paraconid, a "V"-shaped hypoconid with a hypoconulid and entoconid present, and a metaconid which is directly lingual to the protoconid and broadly connected to it. The mandibles are roughly alike in profile. A long, slender angular process appears on the University of California material of *Gypsonictops* (which is under detailed study at present by Mr. William A. Clemens). A broken area occurs on the posteroventral margin of the jaw and it is likely that a similar angular process was present in *Micropternodus*. On the P^4 of *Gypsonictops* the metacone is beginning to fuse with the paracone, leading to the trenchant ridge characteristic of that tooth in *Micropternodus*. The upper molars have a well-developed posterior cingulum and incipient stylar cusps on the external cingulum. The comparatively low-crowned cheek teeth of *Gypsonictops* present an excellent morphological ancestral type for *Scenopagus* and the Oligocene insectivores under discussion.

Saturnina gracilis from the late Eocene of Europe, considered to be an ancestral shrew by Stehlin (1940), shows some likeness to *Micropternodus* in the upper cheek tooth series P^4 to M^3, but certainly not in detail. Its assignment to the base of the soricoid phylogeny seems a wise one.

The possibility that the Geolabidinae may be descended from insectivores close to the Cretaceous *Gypsonictops* has already been considered in passing by Simpson (1951). McKenna and Simpson (1959) consider that the metacodonts (sensu Geolabidinae of the Erinaceidae, McKenna, in press) originated from a *Scenopagus*-like ancestor. Features common to *Micropternodus* and *Gypsonictops* have been listed. The rostrum and upper dentition of *Micropternodus* were found to exhibit a general similarity to those of the Geolabidinae and *Scenopagus*. It appears that these combined genera (with possibly *Cryptoryctes*, *Arctoryctes*, and the unnamed humeri from the middle Paleocene of Montana and from the middle Miocene of Stewart Spring, Nevada (see Reed and Downs, 1958), constitute a previously unrecognized natural group of insectivores. The known morphology of *Micropternodus* is closer to these genera than that of any other group of insectivores known to me. The evidence is at present too incomplete to name, define, or show the relationships of this group. A more adequate understanding of these forms does not so much require further conjecture on the material at hand, but rather necessitates future exploration and study of micro-vertebrate bearing sediments of the late Cretaceous and early Tertiary of North America.

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A NEW AMERICAN OCCURRENCE OF *HETEROSOREX* GAILLARD*

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ABSTRACT—A jaw of Barstovian age from Oregon resembles *Heterosorex sansaniensis* (Lartet) and is probably a new North American species of that genus. *Domnina compressa* Galbreath is a primitive heterosoricine and should be referred to the genus *Heterosorex*.

INTRODUCTION

A PARTIAL lower jaw from a Mascall formation equivalent (Barstovian) in southern Oregon, represents a North American species of the Soricid genus *Heterosorex* Gaillard, until recently recorded only from Europe. The Oregon jaw closely resembles the Vindobonian and Pontian species *Heterosorex sansaniensis* (Lartet), but appears to be somewhat more primitive, especially in the larger size of the three premolars.

A jaw fragment of Crellan age from Colorado, described by E. C. Galbreath (1953) as *Domnina compressa*, appears to be an early member of the heterosoricine lineage, resembling *H.* aff. *Neumayrianus* (Viret & Zapfe, 1951) from the Stampian of Switzerland. It is suggested below that Galbreath's species be transferred to the genus *Heterosorex*.

The Oregon jaw was collected by F. B. Van Houten, and was generously donated by him to the Museum of Natural History of the University of Oregon. Dr. J. Arnold Shotwell, of that institution, kindly loaned the specimen to the University of California Museum of Paleontology for study.

The present work was begun in connection with a seminar directed by Dr. Malcolm C. McKenna, whose advice and aid have been invaluable. I also wish to thank Dr. R. W. Wilson for the loan of the type specimen of "*Domnina compressa*," and Dr. J. T. Gregory for allowing me to consult his description of the Flint Hill *Heterosorex* specimen.

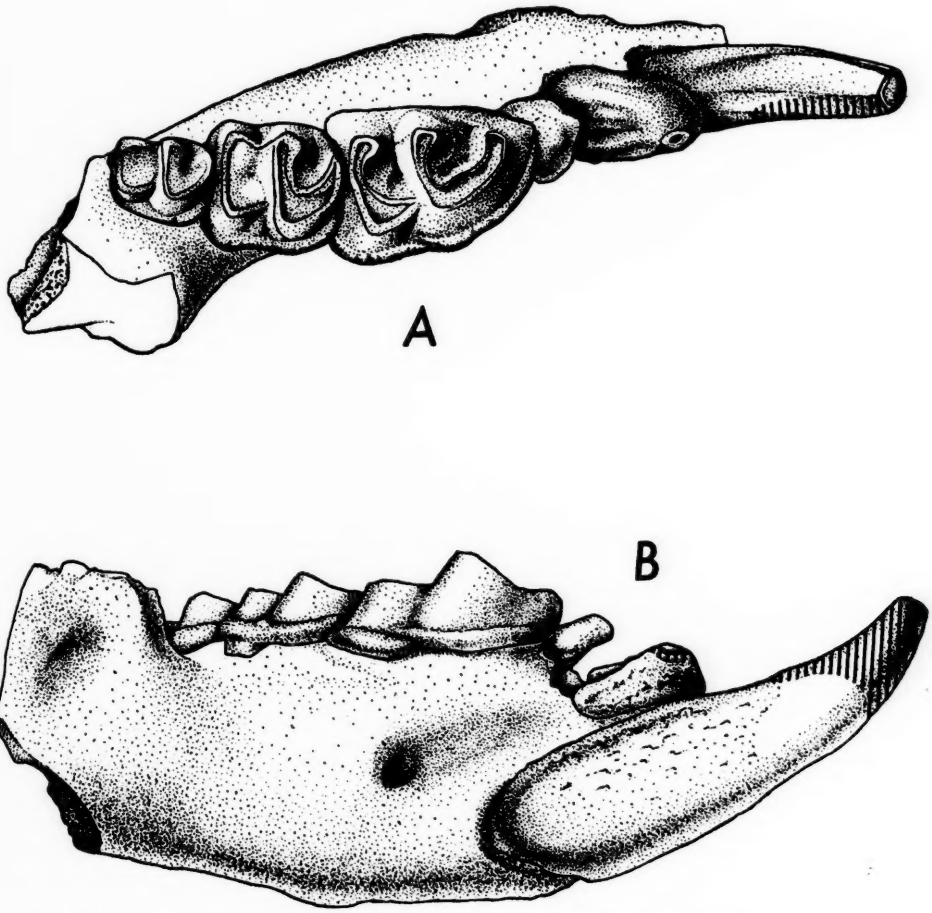
The illustrations are the excellent work of Howard Hamman.

* A contribution from the University of California Museum of Paleontology.

PREVIOUS STUDIES

The genus *Heterosorex* was defined by Gaillard (1915) for a mandible and the facial portion of a skull from La Grive Saint-Alban, which he named *Heterosorex delphinensis*. Stromer (1928) recognized the identity of *Heterosorex delphinensis* Gaillard with *Trimylus schlosseri* Roger 1885, based on a broken mandible with the incisor from the Flinz of Bavaria, and *Sorex sansaniensis* Lartet 1851. Considering Lartet's diagnosis insufficient, and believing the type specimen to have been lost, he decided that Roger's *Trimylus schlosseri* was the valid name of the species. The problem was reviewed by Viret & Zapfe (1951). They considered *Trimylus schlosseri* a *nomen vanum*, based on insufficient material. Having found a mandible fragment with M_{1-2}, which they believed to be Lartet's type specimen of *Sorex sansaniensis*, they concluded that the proper name for the species is *Heterosorex sansaniensis* (Lartet). They also referred to the genus *Heterosorex* a jaw from the Stampian of Rickenbach, which they suggested may be conspecific with *Sorex Neumayrianus* Schlosser 1887. Viret and Zapfe (ibid.) proposed the subfamily Heterosoricinae to include *Heterosorex* Gaillard and possibly *Amblycoptus oligodon* Kormos 1926.

Hetersorex was long thought to have possessed two cheek teeth anterior to the molars. Two alveoli appeared in this space, which Gaillard considered to be those of the canine and one premolar, and later workers thought represented two premolars. In 1952, Crusafont collected a specimen in the Pontian of Vallés-Penedés with three premolars in place. The crucial portion of this specimen was accidentally destroyed, but in



TEXT-FIG. *1*—*Heterosorex* sp. U.O. no. 10486. Right horizontal ramus of mandible, with I, P_1, P_4, M_{1-3}. *A*, occlusal view. *B*, lateral view. ×10.

1957 he found, in the Vindobonian beds of the same area, a mandible whose right ramus showed the usual two alveoli, but whose left ramus bore three small premolars, demonstrating that the two posterior premolars occupied essentially a single alveolus (Crusafont 1957).

Occurrences of *Heterosorex* in North America are just beginning to come to light. A mandible from the Flint Hill fauna of South Dakota is identified as *Heterosorex* by J. T. Gregory and R. A. Stirton (MS.). R. W. Wilson reports (pers. com. to M. C. McKenna) abundant *Heterosorex* material in an unpublished Hemingfordian fauna from the middle Miocene of Northeastern Colorado.

Subfamily HETEROSORICINAE
Viret & Zapfe 1951
Genus HETEROSOREX Gaillard 1915
HETEROSOREX sp.
Text-fig. 1

Material.—Horizontal ramus of a right lower jaw, with incisor, two remaining out of three original premolars, and three molars in place; ascending ramus missing. P_2 was originally present in the specimen, but was

lost in the course of preparation. U.O. 10486.

Locality.—Lake Co., Oregon. 42°03′30″N, 119°34′30″W. 5 miles SW of south end of Guano Lake. Boise (V-2) Sectional Aeronautical chart.

Description.—Mandible: Jaw short and stout, in contrast to soricines, but in agreement with other heterosoricines; ascending ramus arising lateral to M_3; prominent raised muscle scar (for digastric muscle?) on the ventral border of the ramus below the anterior end of M_2; large mental foramen near the mid-height of the ramus, under the talonid of M_1; shallow depression extending forward from the mental foramen between M_1 and the base of the incisor; masseteric fossa with a small deep pit; mandibular foramen in line with the base of the molar row; small foramen on the ventral edge of the lingual side of the jaw, below the metaconid of M_2.

Dentition: Dental formula $\frac{\overline{1-3}}{}\ \frac{\overline{3}}{}$; the teeth present are presumed to be I_4, $P_{1,2,4}$, and M_{1-3} (following homologies proposed for *Sorex* by Ärnbäck-Christie-Linde, 1912).

Incisor large, procumbent, and rooted, with a heavy base extending back under the anterior end of M_1; distal half subtriangular in cross section, with the dorsal side flattened; enamel thick and irregularly crenulated on the lateral side of the tooth for the basal two-thirds of its length; enamel pigmented a deep red-brown for a distance of 1 mm. (on the anterior side) to 2 mm. (on the dorsolateral edge) from the point of the tooth.

Premolar teeth small and procumbent, crowded together between the base of the incisor and the first molar; P_1 much larger than P_4; the missing P_2 probably smaller than P_4 (as in Crusafont's specimen of *H. sansaniensis*). P_1 lying against the dorsal side of the incisor; enamel of the labial side crenulated like that of the incisor below; tip

TABLE 1—MEASUREMENTS OF SPECIES OF *Heterosorex* AND *Domina* (IN MILLIMETERS)

		a	b	c	d	e	f	g	h	i
	Length, 1–M_3	12.0		12.0*	12.3					
	Length, M_1–M_3	5.8	5.2–6.0	6.4*	6.4	4.9	4.5	4.4	5.4–5.8	4.8
Depth of ramus	under M_1				3.4	2.5	2.3*	2.3	2.2–2.5	ca. 2.0
	under M_2				3.6	2.7	2.4*	2.4	2.5	
	under M_3				3.3	2.4	2.3*	2.2		
	I, length			8.0*	7.3					
	P_1, length			1.1*	2.1					
	width				1.5					
	P_2, length			.3*						
	P_4, length			.5*	1.4				1.3	
	width				1.4				1.2	
	M_1, length	2.2	2.2–2.6	2.6*	3.3	1.9	2.0*	2.0	2.2–2.5	1.8
	width			2.0	2.2	1.3		1.4	1.4–1.5	1.2
	M_2, length	1.9	1.5–2.0	2.5*	2.1	1.6	1.6*	1.6	1.8–2.1	1.5
	width			2.0*	1.8	1.1		1.2	1.2–1.4	1.1
	M_3, length	1.7	1.0–1.6	1.4*	1.5	1.2	1.2*	1.3	1.5–1.8	1.3
	width			1.0	1.2	.9		.9	1.1–1.2	.8

a. *Heterosorex sansaniensis.* Gaillard 1915, *passim.*
b. *Heterosorex sansaniensis.* Viret & Zapfe 1951, p. 424.
c. *Heterosorex sansaniensis.* Crusafont 1957, pp. 78–79.
d. *Heterosorex* sp. Oregon specimen. U.C. 10486.
e. *Heterosorex* sp. Flint Hill specimen. U.C.M.P. 37270.
f. *Heterosorex* aff. *Neumayrianus.* Viret & Zapfe 1951, p. 425.
g. *Heterosorex compressus.* Galbreath 1953, p. 47.
h. *Domnina gradata.* Patterson & McGrew 1937, p. 256.
i. *Domnina thompsoni.* Simpson 1941, p. 2.

* Approximate measurements, taken from illustrations.

of the tooth slightly pigmented. The posterodorsal side of P_1 shows a deep valley, between lateral bulges of enamel, and the antero-ventral side of P_4 shows a similar condition. Alveolus of P_2 confluent with that of P_4. P_4 a small, depressed tooth arising at about a 45° angle from beneath the anterior end of M_1.

The molar row decreases in size posteriorly from the large, swollen M_1 to the small M_3. The molars show no evidence of pigment, in either natural or ultraviolet light (wavelength not known).

Paraconid of M_1 overhanging P_4; paraconid and metaconid separated by a broad valley, but with a small shelf connecting their lingual bases; metaconid and protoconid nearly equal in height (at this stage of wear, at least), higher than the remaining cusps, and connected by a strong crest, slightly convex toward the rear; protoconid slightly anterior to metaconid; lower crest connecting protoconid and paraconid; narrow valley separating the entoconid from the metaconid, forming a lingual outlet for the talonid basin; entoconid about equal in height with the paraconid; a crest connecting the entoconid with the lower hypoconid, paralleling the posterior crest of the trigonid; hypoconid crest connecting with the trigonid just medially from the protoconid; no hypoconulid; heavy cingulum present, running from below the metaconid along the labial base of the tooth and disappearing under the overlapping M_2; upper surface of the cingulum rough and irregular.

Paraconid of M_2 overhanging posterior side of M_1; paraconid greatly reduced, appearing merely as a rearward loop of the anterior crest, and less widely separated from the metaconid than in M_1; metaconid-protoconid crest straight; talonid much like that of M_1, but valley between metaconid and entoconid shallower; labial cingulum present as in M_1.

M_3 small; trigonid similar to that of M_2, but somewhat more rounded, and valley between metaconid and paraconid much shallower; talonid reduced by wear to a nearly flat, slightly basined heel; wear facets indicate that the small entoconid and hypoconid were only weakly connected; heavy labial cingulum present as in the preceding molars, but somewhat constricted below the protoconid, and ending below the hypoconid.

Discussion.—The Oregon specimen has been compared with illustrations and descriptions of *Heterosorex sansaniensis* (Lartet), particularly the illustrations by Gaillard (1915, figs. 4 & 5) and Crusafont (1957, figs. 1–4) and the description by Viret and Zapfe (1951, p. 424). Unfortunately, no specimens of the European species were available for comparison.

In form, dental formula, and general tooth morphology, there appears to be very little difference between the Oregon specimen and *H. sansaniensis*—certainly none of generic rank. Differences in detail can be seen, however.

The premolars of the Oregon *Heterosorex* are substantially less reduced than those of Crusafont's specimen from Valles-Penedés. Crusafont makes no mention of crenulation or pigmentation of the enamel of the first premolar of his specimen. None of the previously published illustrations show sufficient detail for reliable comparison of the molar teeth. The incisors of the American and European forms appear essentially similar.

Viret and Zapfe mention the presence in *H. sansaniensis* of a depression anterior to the mental foramen like that appearing in the Oregon specimen. The mental foramien of the Oregon jaw is located farther forward, under the talonid of M_1, rather than under the anterior end of M_2 where it appears in Crusafont's illustration.

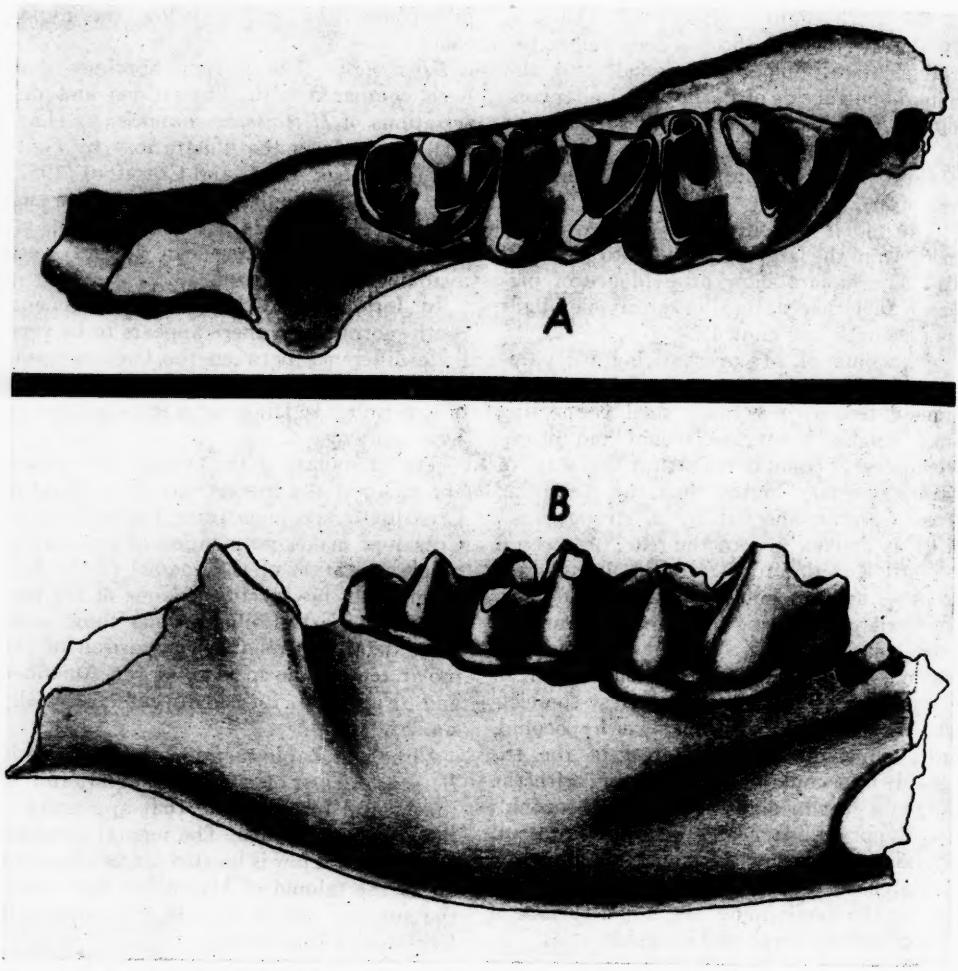
None of the cited authors mentions a foramen on the lingual side of the jaw of *Heterosorex;* however, Gaillard's illustration shows what is probably such a foramen below the posterior end of M_2, farther to the rear than in the Oregon specimen.

The ascending ramus of the Oregon jaw appears to rise farther forward on the mandible than in the specimen from Spain and is much more anteriorly placed than in Gaillard's type specimen.

The Oregon specimen is somewhat larger than the European *Heterosorex* (see Table 1).

In summary, then, the Oregon specimen resembles *Heterosorex sansaniensis* in most particulars, but differs in:

1) lesser reduction of the premolars;



TEXT-FIG. *2*—*Heterosorex compressus* (Galbreath). U.K. no. 8154. Part of right horizontal ramus of mandible with M_{1-3}. *A*, occlusal view. *B*, lateral view. ×15.

2) crenulation and pigmentation of P_4;
3) more anterior position of the mental foramen;
4) more anterior origin of the ascending ramus;
5) larger size.

Very probably, these differences merit specific rank for the Oregon *Heterosorex*. However, in view of the scantiness of the material, and of the fact that two of the important differences are in the premolars, known in only one specimen of the European species, this decision should await the discovery of more material, preferably on both continents.

Affinities of "Domnina compressa."—A specimen (Kans. Univ. Mus. #8154) from the Orellan Cedar Creek member of the White River formation of Colorado, described as *Domnina compressa* by E. C. Galbreath (1933, p. 46–49), appears to be a primitive heterosoricine.

The specimen (Fig. 2) is an incomplete right horizontal ramus, with M_1-M_3 in place, and three premolar alveoli. It is less short and deep than the jaw of the upper Miocene heterosoricines, but somewhat

heavier than that of *Domnina thompsoni* Simpson or *D. gradata* Cope. Its proportions are very similar to those of the Flint Hill *Heterosorex*, and of the jaw illustrated by Viret & Zapfe (ibid., fig. 12) as *Heterosorex* aff. *Neumayrianus*,[1] from the upper Stampian of Rickenbach. There is an elongate depression anterior to the mental foramen, between M_1 and the incisor base, as in *Heterosorex*. The mental foramen is located, as in the Oregon *Heterosorex*, below the talonid of M_1, farther anterior than in the European heterosoricines. A foramen appears on the medial surface of the ramus, below M_2, as in *Heterosorex*.[2]

The base of the incisor extends back as far as the anterior end of M_1, rather than ending anterior to P_1 as in *D. gradata* (Patterson & McGrew 1937, p. 250). The premolar alveoli[3] indicate that the premolar arrangement, although less specialized than that of the upper Miocene heterosoricines, was trending toward a similar condition. The fairly large alveolus of P_4 is located below the overhanging paraconid of M_1. The small alveolus of P_2 is well separated from that of P_4, in contrast to the condition in the upper Miocene species. The alveolus of P_1 is partly broken away, but suggests that P_1 was procumbent, lying against the dorsal side of the incisor.

The molar dentition of the Orellan jaw is basically similar to that of the later heterosoricines, though generally less massive in appearance. The differences that appear are such as might be expected in a primitive member of the heterosoricine lineage. The crests of the trigonids are less strongly developed. The paraconid is less reduced in M_2 and M_3. The lateral width of the talonid is relatively greater. The entoconid is higher and less well separated from the metaconid, but is set off from the posterior crest of the talonid by a faint constriction, in M_1 and M_2. The entoconid of M_3 is transversely compressed, almost bladelike. The hypoconid crest attaches to the trigonid more medially, so that the labial cingulum forms a sloping triangular shelf between the bases of the protoconid and hypoconid, especially in M_3. The basal cingulum is somewhat less strong. A faint ridge ascends the anterior face of the paraconid from the cingulum.

None of the differences noted appear to bar the Orellan species from a position in or near the ancestry of the Miocene heterosoricines. The species should be referred to the genus *Heterosorex* (as *H. compressus*).

The relationship of other species of *Domnina* to the *Heterosorex* lineage is not clear. *Domnina gradata* is barred from a position in the ancestry of *Heterosorex* both by details of the dentition and by the absence of the zygomatic arch, which is retained by *Heterosorex sansaniensis*. In the absence of any known cranial material of *Domnina thompsoni*, it is possible to speculate that this species may have been ancestral to *H. compressus*, as suggested by Galbreath. Thus *Domnina thompsoni* may have been the common ancestor of the lines which led on the one hand to *Domnina gradata*, and on the other to *Heterosorex*.

The structural and temporal gap between *Heterosorex compressus* and the Upper Miocene specimen is partly filled by the Arikareean specimen from Flint Hill (UCMP #37270). Its characteristics are generally intermediate between those of the two species previously discussed, but closer to those of *H. compressus*.

The jaw is slightly larger than that of *H. compressus*, and proportionally heavier. The mental foramen is placed slightly more anteriorly, its posterior border falling below the hypoconid of M_1. The depression anterior to the foramen is more pronounced. The masseteric fossa is shallow. The characters

[1] The illustration is captioned "*Heterosorex* aff. *Neumayri*"—evidently a typographical error, as "*Neumayrianus*" is the form used consistently in the text, and by Schlosser.

[2] A similar foramen appears under M_1 in *Domnina gradata* (W. D. Turnbull, pers. com.). I know of no other soriciods in which such a foramen occurs. However, *Erinaceus* tends to possess a similar foramen, highly variable in position and occurrence. In eight specimens of *E. frontalis* and *E. europaeus* examined in the Univ. of Calif. Museum of Vertabrate Zoology, one lacked the foramen entirely, two had a foramen in one ramus only, one had a diagonal row of several small foramina in each ramus, and the others had a single foramen in each ramus, in various positions below M_2. This may be a primitive vascular route abandoned by most soricoids.

[3] Galbreath states only that "The posterior part of the alveolus of P_4 is preserved." (l.c., p. 47). Actually the alveoli of three premolars are present, and only the anterior part of the alveolus of P_1 is broken away.

of the ascending ramus agree generally with those of Gaillard's specimen.

The proportions of the incisor appear less massive than in the Oregon jaw, more like those which can be inferred for *H. compressus*. The enamel is crenulated, as in the former. The posterior border of the incisor base appears to have been just ahead of the anterior end of M_1, as in *H. compressus;* however breakage in this area makes this difficult to judge, and renders impossible any reliable estimate of the degree of premolar reduction.

The molars differ from those of *H. compressus* mainly in the possession of a heavier external cingulum, more comparable to that of the Barstovian specimen. The cingulum is particularly heavy anterior to the protoconid of M_2, and to a lesser extent of M_1. On M_1, on the contrary, there is little trace of a singulum anterior to the protoconid. The enamel of the molars has a roughened appearance, but this may be due to conditions of preservation.

Phylogenetic position of Heterosorex.—It has been suggested (e.g. Stirton, 1930) that *Heterosorex* is closely related, or even ancestral, to *Blarina* among the living shrews. The relative proportions of the premolars in *Heterosorex* are, however, just the opposite of those in *Blarina*. *Heterosorex* is more probably an independent side branch of the Soricidae, originating from a *Domnina*-like ancestor sometime in the early Oligocene.

SUMMARY

The genus *Heterosorex* is represented in North America by a sequence of forms illustrating an evolutionary progression from the relatively primitive *H. compressus* of the middle Oligocene, to the more specialized upper Miocene specimen from Oregon, resembling the European *H. sansaniensis*. The evidence suggests that North America may well have been the place of origin and the center of evolution of this genus, from a form such as *Domnina thompsoni*.

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JOURNAL OF PALEONTOLOGY, V. 34, NO. 5, P. 957–960, 2 TEXT-FIGS., SEPTEMBER, 1960

VARIANTS AMONG MIDDLE OLIGOCENE RODENTS AND LAGOMORPHS

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ABSTRACT—Dental variations are described in specimens of four species of rodents and one rabbit, mostly considered to be individual variation. One specimen of *Paradjidaumo* is structurally close to *Adjidaumo*. A variant in the structure of the masseter muscle of *Ischyromys troxelli* is recorded. Roots are shown to be formed on the teeth of numerous rabbits referable on a structural basis to *Palaeolagus haydeni*.

INTRODUCTION

A NUMBER of interesting variants were noted during the identification of middle Oligocene rodents and lagomorphs in the Pratt Museum of Amherst College, from the lower Brule Scenic member of South Dakota; from Slim Buttes, S. D.; and from Pawnee Buttes, Weld County, Colorado. These add to our knowledge of individual and age variation in these forms. Of particular interest is the large proportion of the teeth of the rabbit, *Palaeolagus haydeni*, that possess accessory buccal roots on the upper cheek teeth, a feature not previously recognized in this species.

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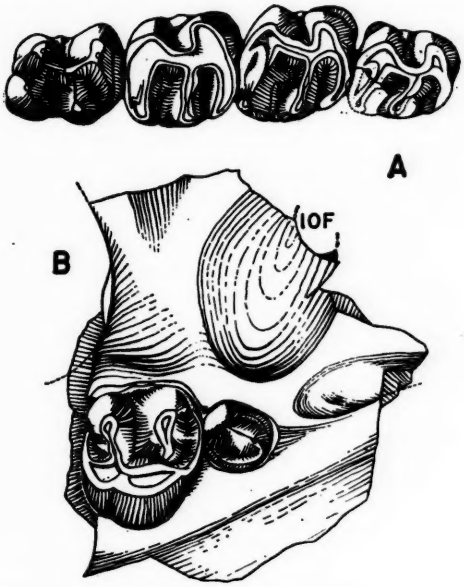
RODENTIA

ISCHYROMYS TYPUS Leidy, 1856

Text-fig. 1A

The teeth of a lower jaw (A.C.M. 10600) from the middle Oligocene of Pawnee Buttes, Colorado, differ from what is normal in this species by possessing a crest extending posteriorly from the center of the metalophid of P_4, M_2 and M_3, reaching the hypolophid at a level below the wear surface (text-fig. 1 A). With wear, an enamel lake would be isolated on M_2, where the crest nearly fills the median valley, and probably on M_3. Such a crest apparently was incipiently present in M_1, though largely obliterated by wear. It is possible that a lake would be isolated on this tooth, after extreme wear. Although this feature has previously been mentioned (Wood, 1937, p. 177) and figured (Leidy, 1869, pl. 26, fig. 5), no very clear illustration has as yet been published. Leidy's figure indicates a somewhat different development of the crests in his specimen, with a crest damming the valley in M_2, whereas as in M_1 and M_3 there are isolated cusps lying in the center of the mesoflexid. There is no evidence at present of any taxonomic value to this feature, and the variability among the different specimens in



TEXT-FIG. 1—*Ischyromys* Leidy. ×5.
A. *I. typus* Leidy, A.C.M. 10600, P_4-M_3 right.
B. *I. troxelli* Wood, A.C.M. 10604, P^{3-4} right. IOF = infraorbital foramen.

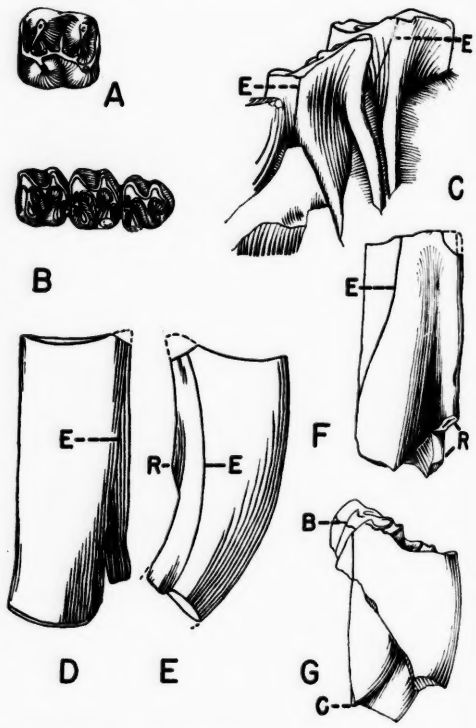
which it occurs suggests the absence of any strong selective value for it, and the probability that it is merely due to a randon recombination of genes within the population, with, probably, variation in the expression of the genes.

ISCHYROMYS TROXELLI Wood, 1937
Text-fig. 1B

A fragmentary maxilla, A.C.M. 10604 from Slim Buttes, South Dakota, is referred to this species on the basis of the shallowness of the pit in front of P^3 and the broad fossa on the anterior side of the zygomatic arch (text-fig. 1B), which are characteristic of this species (Wood, 1937, p. 191). P^3, hitherto unknown for this species, is a large tooth with an elongate central cusp, and strong lingual and anterobuccal cingula. The rugosities for the musculature indicate the development of two separate origins of the masseter, one being confined to the ventral surface of the zygoma, and the second occupying the depression on the masseteric plate in front of the zygoma and ventral to the infraorbital foramen.

EUMYS ELEGANS Leidy, 1856
Text-fig. 2A

As in any collections of material of this species, there is a great deal of minor dental variation. The most significant, evolutionarily speaking, occurs in three isolated specimens of M^2 from the lower part of the Scenic member, about two miles south of Scenic, South Dakota. In these, the main connection of the protocone and paracone is through a strong crest from the paracone to the anterior arm of the protocone, while a subsidiary crest connects the base of the paracone with the posterior arm of the protocone, cutting off a small basin (text-fig. 2A). This latter crest is the usual protoloph of *E. elegans* (Wood, 1937, fig. 57), and the shift in emphasis of the crests is suggestive of the changes characteristic of the somewhat later *E. brachyodus* and *E. exiguus* (Wood, 1937, figs. 61,63). The extremely long anterior cingulum is most like that of *E. exiguus*, but the rest of the pattern (long mesoloph, absence of an ectoloph, and buccal union of the metacone and posterior cingulum) are quite characteristic of *E. elegans*.



TEXT-FIG. 2—Teeth of middle Oligocene rodents and rabbits. ×5.

A. *Eumys elegans* Leidy, A.C.M. 10999, M^2 right.
B. *Paradjidaumo trilophus* (Cope), A.C.M. 10615, M_{1-3} right.
C. *Palaeolagus haydeni* Leidy, A.C.M. 10639, P^{3-4} right, showing buccal roots of type 1 on rear of P^3 and front of P^4. E = limit of enamel.
D. *P. haydeni* Leidy, A.C.M. 10661, M^2 right, showing roots of type 2 forming from ridges. E = limit of enamel.
E. *P. haydeni* Leidy, A.C.M. 10629, P^3 left, type 3. R = ridge; E = limit of enamel.
F. *P. haydeni* Leidy, A.C.M. 10654, M_1 or $_2$ right, anterior view showing roots. R = roots; E = limit of enamel.
G. *P. haydeni* Leidy, A.C.M. 10653, posterior view of P^3 right. B = end of enamel in buccal valley; C = end of enamel in crescentic valley.

PARADJIDAUMO TRILOPHUS (Cope), 1873
Text-fig. 2B

A jaw (A.C.M. 10615) from the lower part of the Scenic member, Scenic, South

Dakota, combines dental features of *Adjidaumo minutus* and of *Paradjidaumo trilophus*, although it clearly must be referred to the latter. The extreme buccal position of the union of the protoconid and anterior cingulum is characteristic of *Paradjidaumo*, but the union of the cingulum and metalophid near the center of the last two molars (text-fig. 2B) is characteristic of *Adjidaumo*. This also occurs on M_3 of A.M.N.H. 9634 (Wood, 1937, p. 241), a specimen referred to *Paradjidaumo minor*. The mesolophids of M_{1-2} are free at their tips, as in *Adjidaumo*, instead of uniting at the distal end with the entoconid, as in *Paradjidaumo*. In M_3, however, such a union has taken place, which characterizes both genera (Wood, 1937, figs. 46,49). This freedom of the mesolophid in M_{1-2} is partly due to lack of wear of this specimen, but in part is real. This type of variant in *Paradjidaumo* is expectable if that genus evolved from *Adjidaumo*, as seems probable, even though the split between the two must have occurred before the Chadron.

LAGOMORPHA
PALAEOLAGUS HAYDENI Leidy, 1856
Text-fig. 2C–G

The very abundant material of this species from the type locality of the Scenic member of the Brule (Bump, 1956, p. 430) gives important additional information on rate of growth of these teeth, areas of nondeposition of enamel, and especially on root formation.

It has been generally accepted (Wood, 1940, p. 278) that one of the differences between the middle Oligocene *P. haydeni* and the lower Oligocene *P. temnodon* is the presence of rooted cheek teeth in the latter and their absence in the former. This gives great interest to the discovery of roots, or traces of roots, in most of the upper teeth of the present collection, both from South Dakota and from Colorado. Roots are rarely present in the lower teeth.

In the upper teeth, roots may be present as long, slender structures, free from the main portion of the crown (type 1, text-fig. 2C). These are similar to the roots of *P. temnodon*, but are much more delicate, being exceptionally fragile. Complete roots have never been seen in isolated teeth, as they are always broken off, but they have been uncovered in several specimens by removal of the bone. A more common condition is the pinching of the buccal side of the tooth, below the level of the enamel cap, into long, slender ridges, which end in a slight rootlet, only a few tenths of a millimeter long (type 2, text-fig. 2D). Still a third variant possesses ridges similar to the second type, but without the rootlets, so that there are at most two separate openings for the pulp cavity at the base of the tooth (type 3, text-fig. 2E). Accessory roots of all types are absent on P^2 and M^3. As shown in table 1, they are most abundant and best developed on P^3, and progressively rarer and less developed to the rear. On P^3, the accessory root is always at the posteroexternal corner; on M^2 always at the anteroexternal corner; while on P^4 and M^1 either or both may be present. The differences do not seem to be associated with the age of the animal (except that roots are not present in completely unworn teeth), but rather seem to be random individual variants. Roots are rare in lower teeth, but have been noted in one specimen (text-fig. 2F).

TABLE 1—NUMBER OF SPECIMENS POSSESSING ROOTS IN UPPER TEETH OF *Palaeolagus haydeni*

	Type 1	Type 2	Type 3	No roots
P^3	6	3	3	1
P^4	2	4	3	6
M^1	1	5	3	3
M^2	0	1	2	6

The most reasonable taxonomic interpretation of these specimens is that *P. haydeni* is directly derived from *P. temnodon*, and that one of the changes involves the elimination of the roots of the cheek teeth. In the earliest populations of *P. haydeni*, minute accessory roots were normally present in the upper molars and rarely in the lowers. Selection for increased hypsodonty resulted in the rapid elimination of these structures. The presence of rooted teeth in the material from Pawnee Buttes leaves open the question as to whether this is a very early Brulean population; a primitive isolate surviving to later times; or whether roots are very generally present in all populations of *P.*

haydeni, but have not yet been recognized.

The enamel is deposited as a cap of very limited extent on the buccal side of the upper and lingual side of the lower cheek teeth. In an unworn P^4, A.C.M. 10659, the enamel extends only 0.8 mm. down this side. For this reason, wear very quickly extends below the level of the enamel on one side. On the other three sides of the teeth, the enamel organ continued to function for a much longer period. Progressively, however, the area of nondeposition of enamel is enlarged. Initially, this enlargement is gradual, so that the edge of the enamel forms a nearly vertical line on the side of the tooth (text-fig. 2D–F), but in older individuals the area of nondeposition expands more rapidly, and the edge of the enamel bends sharply toward the lingual side of the upper and buccal side of the lower cheek teeth (text-fig. 2F). No specimens have been seen in which there was not a complete covering of enamel on the buccal side of the upper and lingual side of the lower teeth. In moderately worn teeth, the border of the enamel runs vertically down the side of the tooth, and the base of the enamel is horizontal on three sides of the crown (text-fig. 2D). This merely means that the crown is still actively growing, and is an indication of the extreme hypsodonty in this species. The total height of crown of an upper molar during the lifetime of an individual would apparently amount to about 15 mm. Since most of this is worn away by the time an individual is senescent, it would indicate cheek tooth abrasion at a rate as much as 0.6 mm. per month (assuming a maximum life of two years). Corroborative evidence is given by A.C.M. 10653, a broken but slightly worn P^4, in which the base of the enamel surrounding the buccal and crescentic valleys can be seen (text-fig. 2G; B and C). As the crescentic valley is eliminated early in the life of this species, wear was obviously rapid.

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AN EARLY PLIOCENE FAUNA FROM MISSION, SOUTH DAKOTA

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Boise, Idaho[1]

ABSTRACT—A Clarendonian mammalian fauna from a sand pit near Mission, South Dakota, is described. The material comprising this fauna was collected during the operation of the sand pit for highway construction select borrow. Due to these operations the remains, although abundant, are quite fragmentary. The fauna is a correlative of the Big Spring Canyon fauna from Martin, South Dakota. A new species of camel, *Procamelus foxi*, is described.

INTRODUCTION

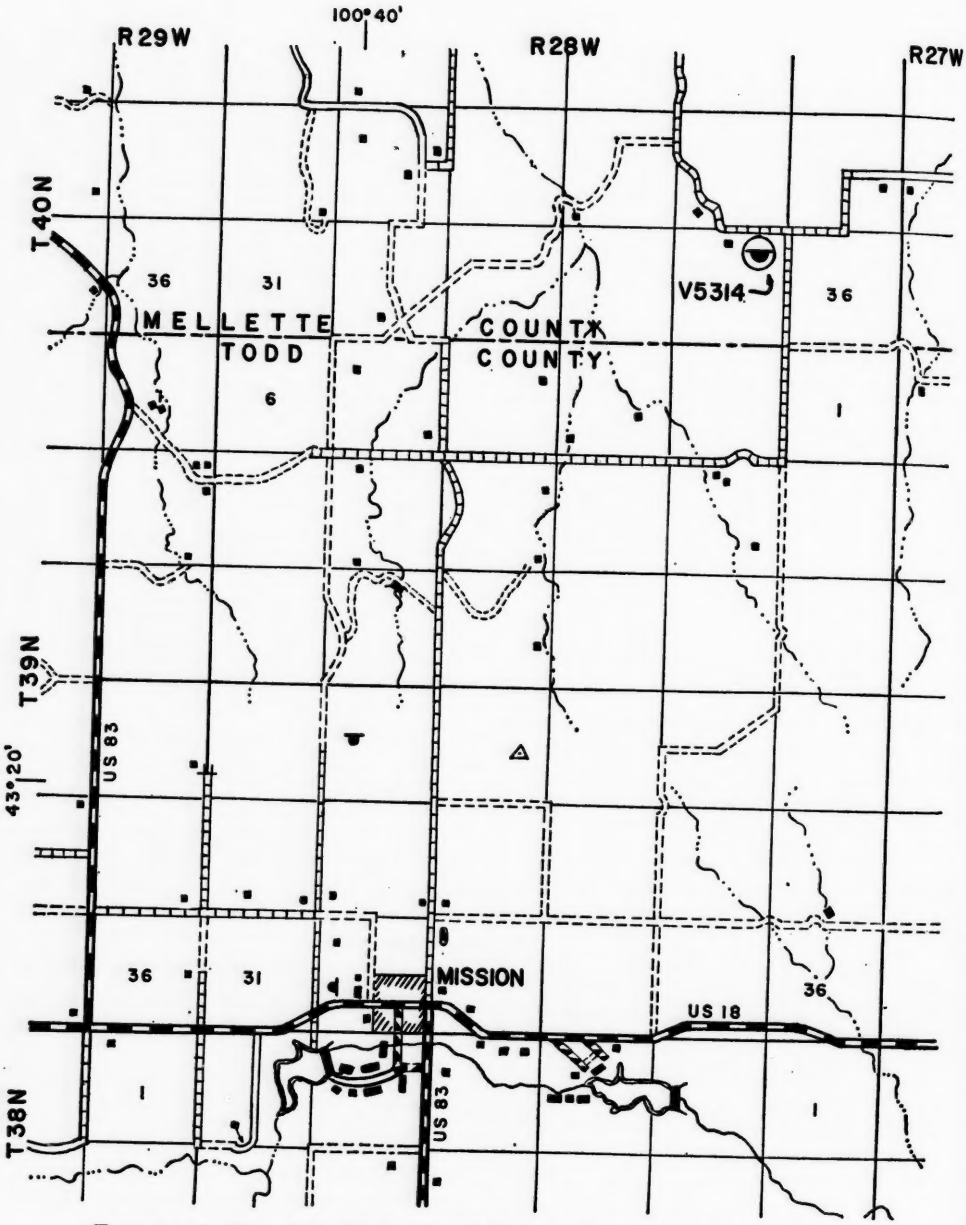
DEPOSITS containing vertebrate fossils of early Pliocene age are found in scattered outcrops along the southern border of South Dakota in a belt that extends from Pine Ridge, on the west, to the Missouri River, on the east. These deposits are the tattered remnants of a series of flood plain and stream channel sediments that at one time must have formed an almost continuous blanket over much of this area. The Pine Ridge escarpment which marks the northern edge of the High Plains has its outliers in isolated patches of Miocene outcrops that extend out over small areas of the White River Badlands. The continuous Pliocene blanket of the Niobrara River area has similar outliers in the valleys of the Little White River, and the lower reaches and tributaries of the White River.

The Mission fauna was obtained from a sand pit on the Thomas Fox ranch in the NW¼ of the NE¼ of Section 35, T 40 N, R 28 W, Melette County, South Dakota. Our attention was first drawn to this locality by the Summit Construction Company of Rapid City, South Dakota, when they sent the Museum of Geology a handful of horse teeth from the sand pit. A series of visits to the pit during the operations of the construction company and several subsequent periods of prospecting developed the present collections.

Most of the collection was made while the pit was being worked for select borrow for highway construction. Sand and gravel were bull-dozed into a hopper and, by means of a conveyor belt, were fed onto a vibrating screen. Trucks and trailers were loaded with the desired grades of material that fell through the screens, and the residue was discarded by means of a chute. In order to retrieve the fossils, a collector stood at the bottom of the chute with a garden rake and salvaged the specimens before they were destroyed by falling rock. Needless to say, lumps and bruises were the fruit of overzealous collecting when a series of specimens came down the chute in a short rush. During later operations, a crusher was used in the pit, and the collector stood on a walkway beside the vibrating screen and grabbed the specimens before they were devoured by the mechanism.

The deposit is unconsolidated except for local pockets that have been cemented by "caliche" and other limy cements. This remnant covers about five acres and is about twenty-five feet in thickness. The beds are typical stream channel deposits with interbedded lenses of fine garnetiferous sands within the layers of gravel and cobbles. The composition of this material indicates that the Black Hills were a probable source of the sediments. This particular deposit is indistinguishable from other outcrops in the area, but this is the only one from which any number of fossil remains has been recovered. It is entirely possible that early collectors visited this site. Fragments are fairly abundant on the surface of this channel in the adjacent section to the north. Such occurrences may have attracted early collectors, but, since their locality descriptions are often painted with a broad brush (a failing not entirely confined to the pioneers of Great Plains collecting), it is impossible to determine whether or not this site is in reality a classic locality of the past.

[1] The greater portion of this paper was written while the author was Curator of Vertebrate Paleontology of the Museum of Geology, South Dakota School of Mines and Technology, Rapid City, South Dakota.



TEXT-FIG. *1*—Map of the Mission, South Dakota area showing the location of the Fox sand pit locality, V5314.

ACKNOWLEDGMENTS

The study of the Mission fauna was made possible through NSF Grant "NSF-G2168." My thanks are extended to Mr. and Mrs. Thomas Fox for granting permission to collect from this site and to camp on their property; to the officers and employees of the Summit Construction Company of Rapid City, with particular appreciation to W. C. Rounds, Floyd A. Collins, and Gus Schultz; Roman Welfl of the South Dakota State Highway Department; and to the Zeitner family of Mission, South Dakota, all of whom aided in making this collection; finally to Dr. Morton Green of the South Dakota School of Mines and Technology, Charles Gremmels of Hot Springs, South Dakota, Dr. Mary Dawson of Smith College, and to my son, Philo Macdonald, who aided in making the greater part of this collection. The drawings were made by Mildred Ahrlin of Rapid City, South Dakota, and the map and chart were drawn by my wife, Eileen. Dr. Green rendered a final service by aiding in the preparation of the manuscript.

THE AGE OF THE MISSION FAUNA

In general the Mission Fauna is a correlative of the Big Spring Canyon Fauna. *Aelurodon taxoides*, *A.* cf. *inflatus*, *Nannippus* cf. *gratus*, *Teleoceras* cf. *fossiger*, *Procamelus grandis*, and *Pliauchenia* cf. *magnifornis* are found in both faunas. *Pliocyon walkerae* is from the Clarendon of Texas. The type of *Tomarctus euthos* is from the Burge fauna of Nebraska which suggests an older element in the Mission fauna. The method of collecting prevented any stratigraphic control which in turn prevents a definite opinion that this is not a mixed fauna. The presence of two jaw fragments of a small oreodon, similar to the type found in the early Miocene Wounded Knee fauna in the Porcupine Creek area to the west, is evidence that some reworking may have taken place.

FAUNAL LIST

Rodentia
- *Mylagaulus* sp.

Carnivora
- *Tomarctus euthos* (McGrew)
- *Aelurodon taxoides* Hatcher
- *Aelurodon* cf. *inflatus*
- *Pliocyon walkerae* Johnson and Christian

Proboscidea
- *Gomphotherium* sp.

Perissodactyla
- *Hypohippus* sp.
- *Neohipparion* cf. *occidentale* and/or *whitneyi*
- *Neohipparion* sp.
- *Pliohippus* sp.
- *Pliohippus* cf. *martini*
- *Nannippus* cf. *gratus*
- *Tapirus* sp.
- *Teleoceras* cf. *fossiger*

Artiodactyla
- *Prosthennops* sp.
- *Ustatochoerus* sp.
- *Protolabis* sp.
- *Procamelus grandis* Gregory
- *Procamelus foxi* n. sp.
- *Procamelus* or *Pliauchenia* sp.
- *Pliauchenia* cf. *magnifontis*
- *Paracamelus* or *Aepycamelus* sp.
- *Cosoryx* sp.

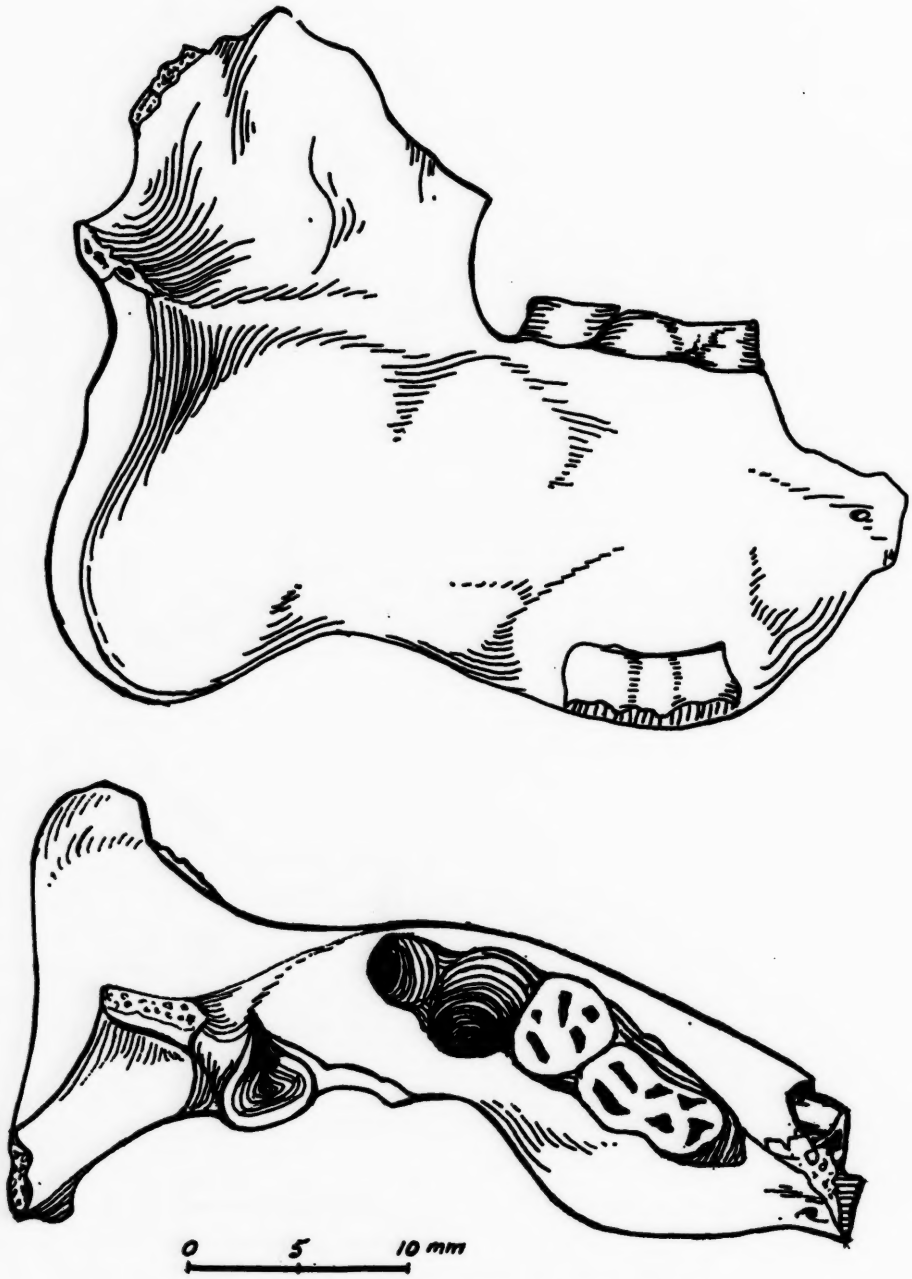
DESCRIPTION OF THE MISSION FAUNA

RODENTIA
MYLAGAULIDAE
MYLAGAULUS sp.
Text-fig. 2

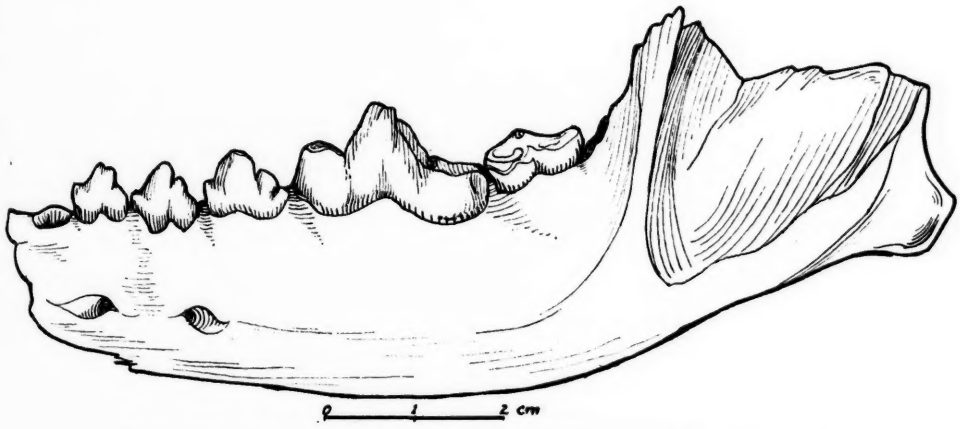
53289 Humerus[2]
552 Right ramus with root of incisor, dP_4, M_1, the alveoli of M_{2-3}, the unerupted P_4.

The triangular incisor is broken in the alveolus and extends under the cheek tooth row until it rises high into the ascending ramus. The dP_4 is elongated antero-posteriorly, two rooted, and in an advanced stage of wear; there are six lakes on the crown; the anterior lake is "V" shaped; this lake is followed by two paired lakes, a small single lake, and a posterior pair of elongated lakes. M_1 is nearly circular with five lakes: two small anterior lakes, an elongated transverse lingual lake, a chevron shaped labial lake, and a short medial posterior lake. At a slightly greater stage of wear the chevron shaped lake will be divided into two lakes due to the separation of the anterior end. At the very last stages of wear the transverse lingual lake will also divide into two separate lakes. The alveolus for M_2 is nearly cir-

[2] All specimen numbers, unless otherwise noted, are of the Museum of Geology, South Dakota School of Mines and Technology. There are some who will be critical of the fact that I am listing all specimens or "publishing my field notes," but I believe that a complete listing of material is of value to future students.



TEXT-FIG. 2—*Mylagaulus* sp. SDSM 552, right ramus. ×3.



TEXT-FIG. 3—*Tomarctus euthos* (McGrew) SDSM 53250, left ramus. ×1.2.

cular and indicates that this tooth was slightly larger than M_1. The alveolus for M_3 is tilted anteriorly and is slightly more than half the diameter of the alveolus for M_2. P_4 is unerupted and unexposed except where a portion of the greatly distorted wall of the ramus has been broken away over the base of the tooth. The wall of the ramus has been greatly expanded on the labial side and the outline of the P_4 is readily observed. Later eruption of the P_4 would force both the dP_4 and the M_1 out of their alveoli.

TABLE OF MEASUREMENTS

	Antero-posterior diameter	Transverse diameter
dP_4	6.4 mm.	3.3 mm.
M_1	4.5 mm.	4.2 mm.
M_2 (alveolus)	3.5 mm.	4.6 mm.
M_3 (alveolus)	2.8 mm.	2.6 mm.

CARNIVORA
CANIDAE

The dogs are surprisingly abundant in the Mission fauna, and it is of particular interest that they are the only carnivores known from the assemblage. Three genera have been found. The large *Pliocyon walkerae* Johnson and Christian is the most abundant form. The Borophagine dog *Aelurodon* is represented by two species: several specimens are referable to *A. taxoides* Hatcher (1894), and a single mandible may be referable to *A. inflatus* VanderHoof and Gregory (1940). The medium sized dogs are represented by a lower jaw of *Tomarctus euthos* (McGrew, 1935).

The complete absence of small dogs and all other carnivores from this fauna probably must be due to pure chance. A similar assemblage, on a smaller scale, from the early Clarendonian Black Hawk Ranch fauna (Macdonald, 1948) contains large and medium sized dogs, two foxes, two large cats, and a Bassariscus. The method of collecting at this site may account for the paucity of small animals, but it does not explain the absence of the larger cats which must have been fairly abundant in this area.

Tomarctus euthos (McGrew)
Text-fig. 3

53280 Left mandible with P_2-M_2 and the alveoli for P_1 and M_3.

This jaw is essentially identical to the jaw (UCMP 32242) from the Burge (Burge) fauna that VanderHoof and Gregory (1940, figures 7 and 8) referred to *Tomarctus euthos* (McGrew).

The P_1 is single rooted; P_{2-4} are double rooted and increase in size and complexity. Each premolar has an anterior cingular cusp, a principal cusp, a posterior accessory cusp, and a posterior cingular cusp; the principal cusp is anterior to the center of the tooth. M_1 has a strong metaconid although not as prominent as either of the Burge specimens

Tomarctus euthos (McGrew)

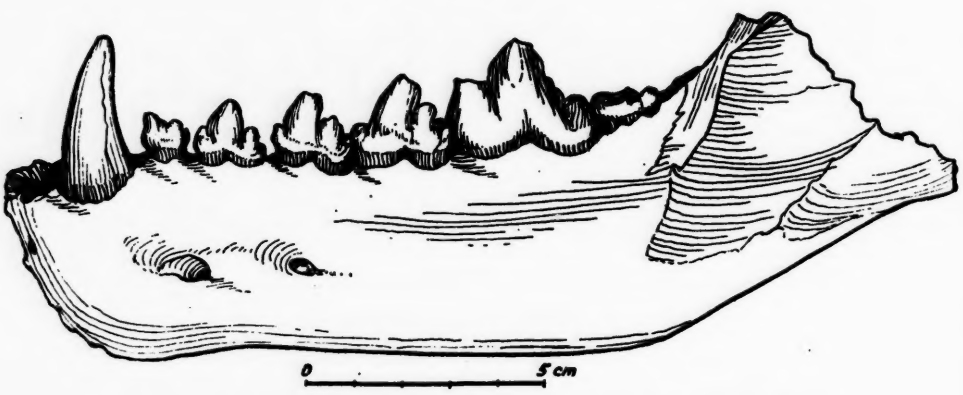
TABLE OF MEASUREMENTS

	SDSM 53280	UCMP* 32242	UCMP* 33864
Canine			
Antero-posterior diameter	8.3		
Transverse diameter	6.4		
P_1 (alveolus only)			
Antero-posterior diameter	4.5		
Transverse diameter	3.5		
P_2 Antero-posterior diameter	6.3	6.5	7.1
Transverse diameter	3.9	3.8	4.1
P_3 Antero-posterior diameter	8.0	7.7	
Transverse diameter	4.5	4.5	
P_4 Antero-posterior diameter	9.6	10.2	10.4
Transverse diameter	5.5	5.8	5.7
M_1 Antero-posterior diameter	19.6	20.1	20.2
Transverse diameter	8.4	8.1	8.3
M_2 Antero-posterior diameter	9.8		10.3
Transverse diameter	6.7		6.6
P_2–M_2	53.4		57.5

* From the Burge fauna.

at hand; the talonid is double basined with the typical *Tomarctus* cross-connection between the entoconid and the hypoconid separating the anterior and posterior basins. M_2 has a small trigonid with the paraconid the smallest cusp; there is a triangular antero-labial ledge extending from the base of the paraconid and the protoconid that "squares off" the anterior end of the tooth; the talonid is equal to the trigonid in size with a well developed hypoconid and a small entoconid and entoconulid which form an enamel ridge around the basin. The M_3 is represented by a double alveolus, indicating that this tooth was rather long and narrow.

There seems to be no doubt that this jaw is co-specific with the Burge (Burge) material. It should provide a positive correlation between the two faunas without further consideration. However, due to the nature of the accumulation of the Mission fauna and the method of collection, we have no positive assurance as to the coexistence of all of the elements of the Mission fauna. A single jarring note in faunal assemblage is the presence of two jaw fragments of a Leptauchenid. While these fragments are surely reworked, it opens the door to the suspicion that other elements may also have been redeposited.



TEXT-FIG. 4—*Aelurodon taxoides* Hatcher SDSM 553, left ramus. ×0.64.

Aelurodon taxoides

TABLE OF MEASUREMENTS

	Type*	*A. magnus* Type*	UCMP 32588 Right	UCMP 32588 Left	553	53279	53278	572	573	53277	5652 Right	5652 Left
Canine, a-p diameter				13.2	16.0							
Canine, trans. diameter				11.0	12.8							
P_1, greatest a-p diameter				9.2	10.7							
P_1, greatest tr. diameter				7.0	7.8							
P_2, greatest a-p diameter			12.4	12.2	14.8	12.5	15.6					
P_2, greatest tr. diameter			8.4	8.4	8.3	7.2	8.6					
P_3, greatest a-p diameter			14.7	14.6	18.4		15.8		18.1			
P_3, greatest tr. diameter			9.5	9.6	9.5		10.5		9.7			
P_4, greatest a-p diameter	22.0	21.0	18.5	18.1	21.4	17.3						
P_4, greatest tr. diameter			10.8	10.8	11.0	10.2						
M_1, greatest a-p diameter	34.0	32.0	29.8	29.5	31.3					32.2		
M_1, greatest tr. diameter			12.7	12.2	13.4					13.3		
M_2, greatest a-p diameter	12.0	14.0	12.2	12.4	13.5			?11.0				
M_2, greatest tr. diameter			8.8	8.9	9.5			? 8.7				
M_3, greatest a-p diameter	8.0	9.0						? 7.7				
M_3, greatest tr. diameter								? 5.5				
P^3, greatest a-p diameter											18.5	
P^3, greatest tr. diameter											9.6	
P^4, greatest a-p diameter											27.8	28.5
P^4, greatest tr. diameter											14.8	15.7
M^1, greatest a-p diameter												16.8
M^1, greatest tr. diameter												19.6
M^2, greatest a-p diameter											7.7	7.6
M^2, greatest tr. diameter											11.1	11.4

* After original author.

AELURODON TAXOIDES Hatcher
Text-fig. 4

53277 Right mandible with Canine and M_1, roots of P_{1-4}.
53278 Fragment of right mandible with P_{2-3} and the alveolus for P_1.
53279 Fragment of right mandible with P_3 and P_4, alveoli for P_1 and P_2.
553 Left mandible with Canine $-M_3$ and alveoli for I_{1-3} and M_3.
55185 Isolated left P^4.
5652 Partial cranium with P^3-M^2.
572 Fragment of left mandible with M_{2-3}.
573 Fragment of left mandible with Canine and P_4.

The dentition of the complete mandible (553) closely resembles that of the specimen (YPM 10057) that Thorpe (1922) designated as the type of *A. taxoides magnus*. The anterior cingular cusps of the premolars are well developed in Thorpe's specimen in contrast to the condition found in the type of this species and the jaws (UCMP 32588) from Big Spring Canyon (Gregory, 1942).

The premolars of the two small fragments (53278 and 53279) do not have well developed anterior cusps and are intermediate in development between SDSM 553 and UCMP 32588.

The M_1 is seen in two specimens, the jaw with complete dentition and SDSM 53277. In the first of these, the metaconid is well developed, and in the second it is virtually non-existent.

The partial cranium (5652) is certainly referable to this species. The dentition closely resembles that of *A. platyrhinus* Barbour and Cook (1917) which VanderHoof and Gregory (1940) referred to *A. taxoides*. The Mission specimen has a relatively longer M^2 and a somewhat longer talon on the M^1. The P^3 has a large primary cusp, smaller posterior secondary cusp and two accessory cusps, the anterior of these being smaller than the posterior; the cingulum is complete. The P^4 has a greatly reduced protocone, the parastyle is present, but the remainder of the tooth is heavily worn. The M^1 has a subequal paracone and metacone; the protocone is large and the protoconule is larger than the metaconule. The M^2 has a greatly reduced metaconule which is the dominant cusp; the paracone is reduced; the central portion of the tooth is basined, and the entire tooth is almost surrounded by a prominent anterior, posterior, and lingual cingulum.

The variation within this suite of specimens seems to confirm the suggestion that *A. platyrhinus* is synonymous with *A. taxoides*. However, it should be remembered that, although these specimens are all from a

small geographic area, there is no temporal control due to the method of collection.

Aelurodon cf. inflatus

5517 Right mandible with badly broken $P_4 - M_1$, the alveoli for P_{1-2} and M_{2-3}, and the roots of P_3.

This specimen may be referable to *A. inflatus* VanderHoof and Gregory, but due to the poor condition of the teeth it is impossible to make a positive determination. The portion of the talonid of M_1 that is preserved suggests that the hypoconid may be bigger than the entoconid which does not agree with the diagnosis of the species. The overall length of the tooth row is slightly greater than that of the type from Big Spring Canyon, and the P_1–M_1 alveolar length is greater than that of a specimen (53454) in the SDSM & T collections from the type locality.

Table of Measurements

	SDSM 5517	Big Spring Canyon	
		SDSM 53454	UCMP 32328[3]
P_1–M_3 (alveolar)	99.0		90.0
P_2–M_3 (alveolar)	93.6		83.0
P_3–M_3 (alveolar)	80.6		73.0
P_4–M_3 (alveolar)	66.9		60.6
P_4 a–p diameter	17.8	16.5	15.8
transverse diameter	9.9	10.2	10.2
M_1 a–p diameter	30.7	29.0	29.4
transverse diameter	13.5	12.5	12.6

[3] Type, after VanderHoof and Gregory, 1942.

Pliocyon walkerae Johnson and Christian

53274 Left ramus with $P_2 - M_2$ and alveoli for I_1–Canine.
53275 Fragment of right ramus with alveoli for $M_1 - M_3$.
53276 Fragment of left ramus with M_2 and talonid of M_1.
54300 Fragment of right ramus with P_{2-4}.
54301 Isolated P^4 and M^1.
5512 Left palate with waterworn P^{2-4} and alveoli for Canine, P^1, and M^{1-2}.
55186 Right premaxillary with alveoli for I^{1-3}, and Canine.
55214 Right M_2.
5644 Fragment of left ramus with P_4 and alveoli for P_{2-3} and M_{1-3}.
5649 Isolated Canine.
5685 Fragment of left ramus with $P_4 - M_2$.
571 Left ramus with Canine $- M_2$ and the alveoli for I_{1-3} and M_3.
5717 Fragment of left M_1, talonid only.

A comparison between this material and the type of *P. walkerae* Johnson and Christian (1941), from the Clarendon fauna of Texas, indicates that these widely separated geographical forms are co-specific.

The only notable differences between the Texas specimen and the South Dakota material are minor variations in size, particularly the relative and absolute transverse diameter of M^1, the greater size of the paracone of M_1, and, judging from the alveoli, the greater reduction of the M_2.

The dentition of the Mission material is characterized as follows:

M_2 (53214, 53274, 53276, 5685, 571) with distinct trigonid and talonid, separated by a deep lingual sulcus; trigonid bucuspid, paraconid represented by a ridge extending antero-lingually

Pliocyon walkerae

Table of Measurements

	Type	53214	53274	53276	54300	55214	5644	5685	571	5249*	54301
P_2, greatest antero-posterior diameter	11.4		10.8						12.4		
P_2, greatest transverse diameter	9.0		7.4						7.6		
P_3, greatest antero-posterior diameter	17.8		13.0		?15.0				15.4		
P_3, greatest transverse diameter	10.0		7.5		10.4				8.8		
P_4, greatest antero-posterior diameter	21.0		19.7		22.7		?19.5	20.3	19.8	21.4	
P_4, greatest transverse diameter	10.5		11.4		12.4		9.3	10.9	10.3	11.3	
M_1, greatest antero-posterior diameter	38.8		41.2			37.2		41.4	38.0	38.5	
M_1, greatest transverse diameter	16.4		19.1			19.4		19.5	16.4	17.8	
M_2, greatest antero-posterior diameter	24.5	27.4	26.7	27.2				27.3	24.5		
M_2, greatest transverse diameter	17.0	18.9	19.5	19.7				18.9	16.6		
P^4, greatest antero-posterior diameter											30.5
P^4, greatest transverse diameter											?
M^1, greatest antero-posterior diameter											21.6
M^1, greatest transverse diameter											31.4

* *Pliocyon* cf. *medius* from Sinclair Draw, Sioux County, Nebraska.

from paraconid with a slight thickening near the cingulum, metaconid opposite protoconid; talonid with hypoconid only, center of cusp labad to midline.

M_1 (53247, 5685, 571, 5717) with metaconid represented by a small fold in enamel at posterior-lingual corner of protoconid, or absent (571); very large hypoconid; entoconid very small, or absent represented by an expansion of the cingulum opposite the center of the hypoconid.

P_4 (53274, 54300, 5644, 5685, 571) is two or three cusped; principal cusp above or slightly anterior to the center of the tooth; anterior accessory cusp reduced or missing; posterior accessory cusp highly variable: missing, small, or quite large.

P_3 (53274, 54300, 571) with only central (principal) cusp, apex anterior of center of tooth; heel slightly trenchant in 571.

P_2 (53274, 54300, 571) is separated from P_3 by a short diastema; single (principal) cusp anterior to center of tooth, worn only in 54300; slightly trenchant heel.

P_1 not present.

Lower Canine (571) large; recurved; prominent ridge on anterior labial corner.

I_2 (alveolus only; 53274, 571) large; triangular cross section.

I_2 (alveolus only; 53274, 571) reduced; posterior to I_1.

I_1 (alveolus only; 571) greatly reduced, probably missing in some individuals; crowded to symphysis; anterior to labial moiety of I_2.

M^2 (alveolus only; 5512) three rooted; compressed anteroposteriorly; lingual root large; posterior labial root greatly reduced.

M^1 (54301, 5512 (alveolus only)) paracone larger than metacone; small metaconule; large protocone, heavily worn; wide lingual shelf.

P^4 (54301, 5512) deuterocone missing; metacone large, separated from protocone by a deep open carnassial notch.

P^3 (5512) badly water worn; separated from P^4 by a short diastema; set obliquely in maxillary; single cusp.

P^2 (5512) separated from P^3 by short diastema; set obliquely in maxillary; single cusp.

P^1 (alveolus only; 5512) single round root; separated from P^2 by short diastema.

Upper Canine (alveolus only; 5512, 55186) sub-equal with lower Canine.

I^3 (alveolus only; 55186) very large; triangular root.

I^2 (alveolus only; 55186) elongated anteroposteriorly.

I^1 (alveolus only; 55186) reduced, but not as greatly as I_1.

This suite of specimens shows a high degree of minor variability but, taken as a group, certainly represents a single species. Minor cusp variations which, in isolated specimens, might be evaluated as the distinguishing characteristics of different species must, in this instance, be regarded as individual variations within a single population or, at the most, minor progressive changes during a short span of geologic time.

PROBOSCIDEA
GOMPHOTHERIIDAE
GOMPHOTHERIUM sp.
Text-fig. 5

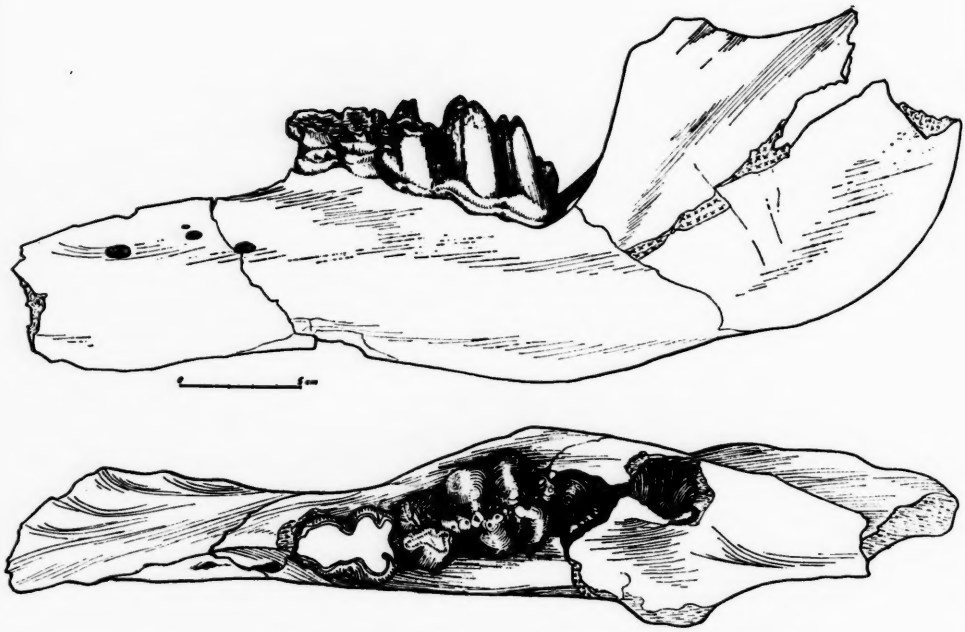
53179 Fragment of right mandible with partly erupted M_3 and the posterior root of M_2.
53182 Isolated P_1.
53183 Isolated dP_3, half of an isolated dP^4, an isolated P^4, and an isolated P_4.
53184 Fragment of a mandible with dP_{2-3}.
53186 Fragment of tusk.
53212 Fragment of left mandible with dP_{3-4} and an unerupted P_1.
53485 Left mandible with completely worn M_3 and a part of the roots of M_2.
5720 Isolated $dP(?)^2$.

One sometimes feels that, like "death and taxes," the fragmentary remains of proboscideans are always with us, and that we don't know quite what to do about them. The unworn M_3 (53179) and the mandible of a very old individual (53485) indicate that these individuals, if not all of the specimens, are referable to *Gomphotherium* sp. The symphysis of 53485 is slightly recurved and the upper portion of the ramus between the symphysis and the M_2 is sharply crested. The unworn M_3 (53179) has $5\frac{1}{2}$ lophs; the 1st and 2nd have single anterior and posterior labial trefoils; the 3rd has an anterior labial trefoil, the 4th and 5th are without trefoils; and the $5\frac{1}{2}$th consists of three small cusps.

PERISSODACTYLA
EQUIDAE
HYPOHIPPUS sp.
Text-fig. 6

55212 Fragment of upper cheek tooth.
55213 Fragment of upper cheek tooth.
5679 Fragment of right mandible with dP_4, unerupted M_1, roots of dP_{2-3}.

The larger of the upper cheek tooth fragments (55212) consists of a badly worn crown with the ectoloph broken away. The metaloph is worn to the base where it joins the cingulum; the cingulum extends from the hypostyle to the labial end of the protoloph where it is broken away. The other upper cheek tooth fragment (55213) is an



TEXT-FIG. 5.—*Gomphotherium* sp. SDSM 53212, left ramus. ×0.33.

unworn protoloph with the parastyle and paracone attached; the cingulum joins the ectoloph to form part of the parastyle.

The jaw fragment (5679) contains the roots of dP_{2-3}, an unworn dP_4, and an unerupted M_1. The dP_4 has a well developed cingulum extending from the hypoconulid to a point near the lingual end of the paralophid; the metastylid and the metaconid are distinctly separated. The unerupted M_1 has been partially exposed showing that the metastylid and the metaconid are only faintly separated at the apex.

The antero-posterior diameter of the dP_4 is 32.8 mm. and the greatest transverse diameter is 17.7 mm.

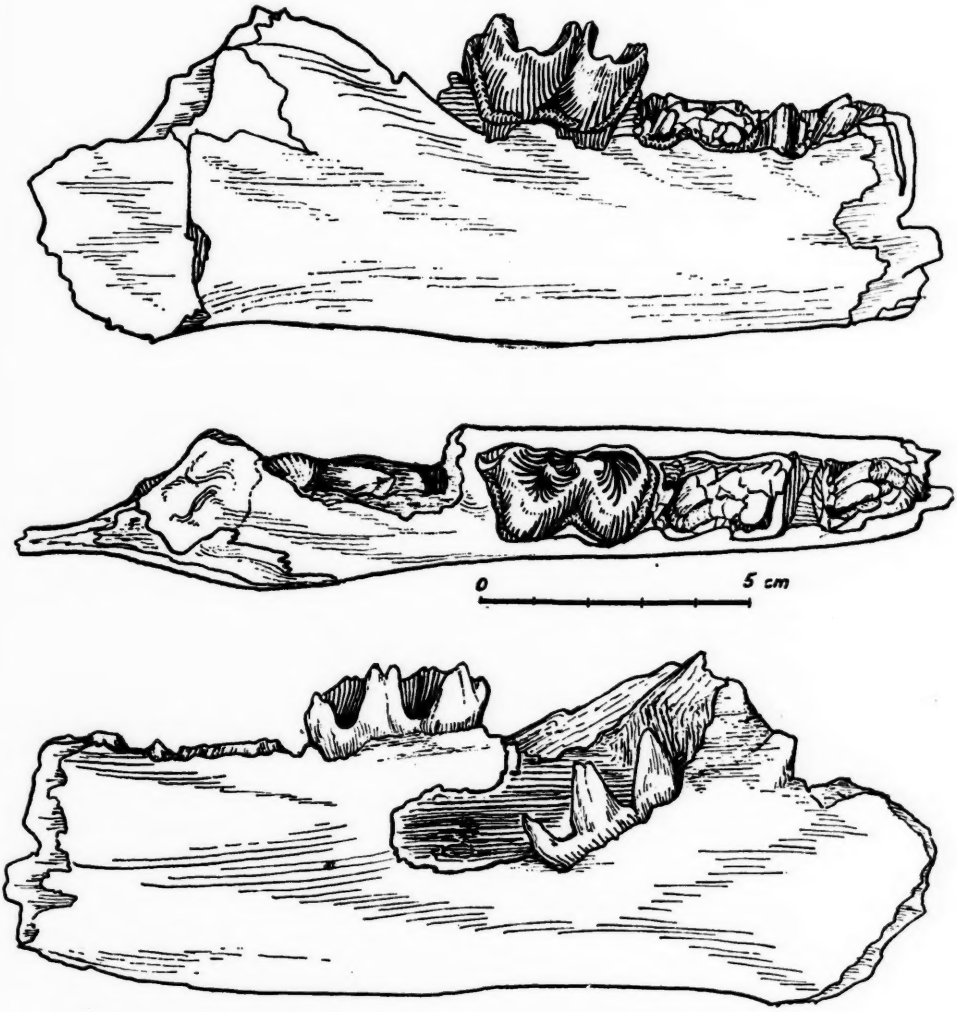
NEOHIPPARION cf. OCCIDENTALE and/or WHITNEYI

53217 156 isolated upper cheek teeth.
53245 100 isolated lower cheek teeth and jaw fragments.

Although *Neohipparion* is the common genus of the Mission fauna, it is represented only by isolated cheek teeth, jaw fragments, and limb bones.

The upper cheek teeth exhibit considerable variation in the size and shape of the crown, shape of the protocone, complication of the fossette borders, and size, shape, and complexity of the pli-caballin fold. Sixty of these teeth which were neither P^2's nor M^3's, unbroken, unabraded, and only moderately worn were measured and studied by Miss Charlotte A. Axsell while gathering data for the preparation of a thesis for the Bachelor of Science degree in Geology at the South Dakota School of Mines and Technology. A plot of these measurements, which included the antero-posterior diameter and the transverse diameter of the crown and the protocone, and histograms of the ratios of these measurements, fail to show any significant breaks that might indicate that more than one species is present in the sand pit.

In his description of the Big Spring Canyon Neohipparions, Gregory (1942, pp. 414–422) suggested that *N. affine* (Leidy) and *N. dolichops* Gidley were synonyms of *N. occidentale* (Leidy). On the other hand, he considered *N. whitneyi* Gidley as a separate species on the basis of the differences in the lengths of the metapodials. Gregory did not



TEXT-FIG. 6—*Hypohippus* sp. SDSM 5679, fragment of right mandible. ×0.73.

consider the size and shape of the protocone or the number of plications of the enamel borders of the fossettes a valid characteristic for specific separation. As the material from Big Spring Canyon falls within the limits of variation found in the Mission fauna, the unity of this material may be in doubt if Gregory's interpretation is correct. A comparison of the metapodials (see below) from these faunas suggests that these species can only be differentiated by metapodial length when isolated teeth are the only other basis for determination.

RECAPITULATION OF *Neohipparion* UPPER CHEEK TOOTH MEASUREMENTS

	Range	Average
Greatest antero-posterior diameter of crown	18.4 –29.3	22.9
Greatest transverse diameter of crown	14.0 –25.9	20.9
Ratios	.73– 1.20	.915
Greatest antero-posterior diameter of protocone	6.0 –11.3	8.08
Greatest transverse diameter of protocone	2.0 – 4.6	3.29
Ratios	.24– .71	.41

The lower cheek teeth of *Neohipparion* are not as common as the uppers; possibly more of these passed through the sizing screens. The cement covering varies from very light to very heavy. The greatest crown height, measured from the base of the protoconid, is 61 mm., the metaconid and the metastylid are generally separated to the base of the teeth. Eight of the lower cheek teeth have small pli-caballinids.

NEOHIPPARION sp.
Text-fig. 7

53187, 53188, 53189, 53192, 53193 } 23 complete metapodials

Numerous complete phalangial, metapodial, carpal, and tarsal elements were collected from the Fox Ranch quarry. Twenty-one of the metapodials may be referred to *Neohipparion* on the basis of size and splint development. Two of the metatarsals (53189) may either represent an extreme individual variation or may belong to an unrecognized form.

The splint scars on the metapodials and the anterior position of the central prominence for the fetlock collateral ligaments show that the splints were tightly appressed to the cannon bone for their entire length.

The metacarpals vary in length from 199.0 mm. to 224.0 mm. These are longer than the specimens (192.0 and 181.0 mm.) that Gregory (1942) recorded from the Big Spring Canyon fauna. The average length of this sample is 212.04 mm. which is close to the type of *N. whitneyi* Gidley (215.0 mm.). The variation of length within the sample is $\pm 11.2\%$ of the average length. A comparison with a suite of *Neohipparion* metacarpals from the Ogallala formation near Valentine, Nebraska, in the collections of the Nebraska State Museum, shows that the same variation is found in both collections. It is, of course, purely coincidental that the variation within the compared samples is 11.2% of the average length in each case. However, it is an indication that the actual variation within the two living populations would not have been of a much greater magnitude.

The ten metatarsals from the Mission fauna that are definitely referable to *Neohipparion* range from 252.0 mm. to 233.5 mm. in length. The average length is 239.6 mm., and the variations amount to 7.7% of the average. A comparative collection from Valentine, Nebraska (Ogallala formation), in the Nebraska State Museum, does not correlate with this dispersion. Nineteen metatarsals were measured with a range of 166.9 mm. to 225.4 mm. in length. However, there seem to be two distinct groups represented by this sample: the smaller, ranging from 166.9 mm. to 184.3 mm., and the larger from 200.4 mm. to 225.4 mm. If the sample is taken as a whole, then the average length is 196.1 mm., and the variation from this figure is 29.8%. If, however, we divide this sample into two groups, the smaller group has an average length of 175.6 mm. with a variation of 9.9%, and the larger group has an average length of 211.0 mm., and the variation is 11.3%. While it must be admitted that this may be considered as figure juggling, the magnitude of variation approaches the figure that we might expect to find.

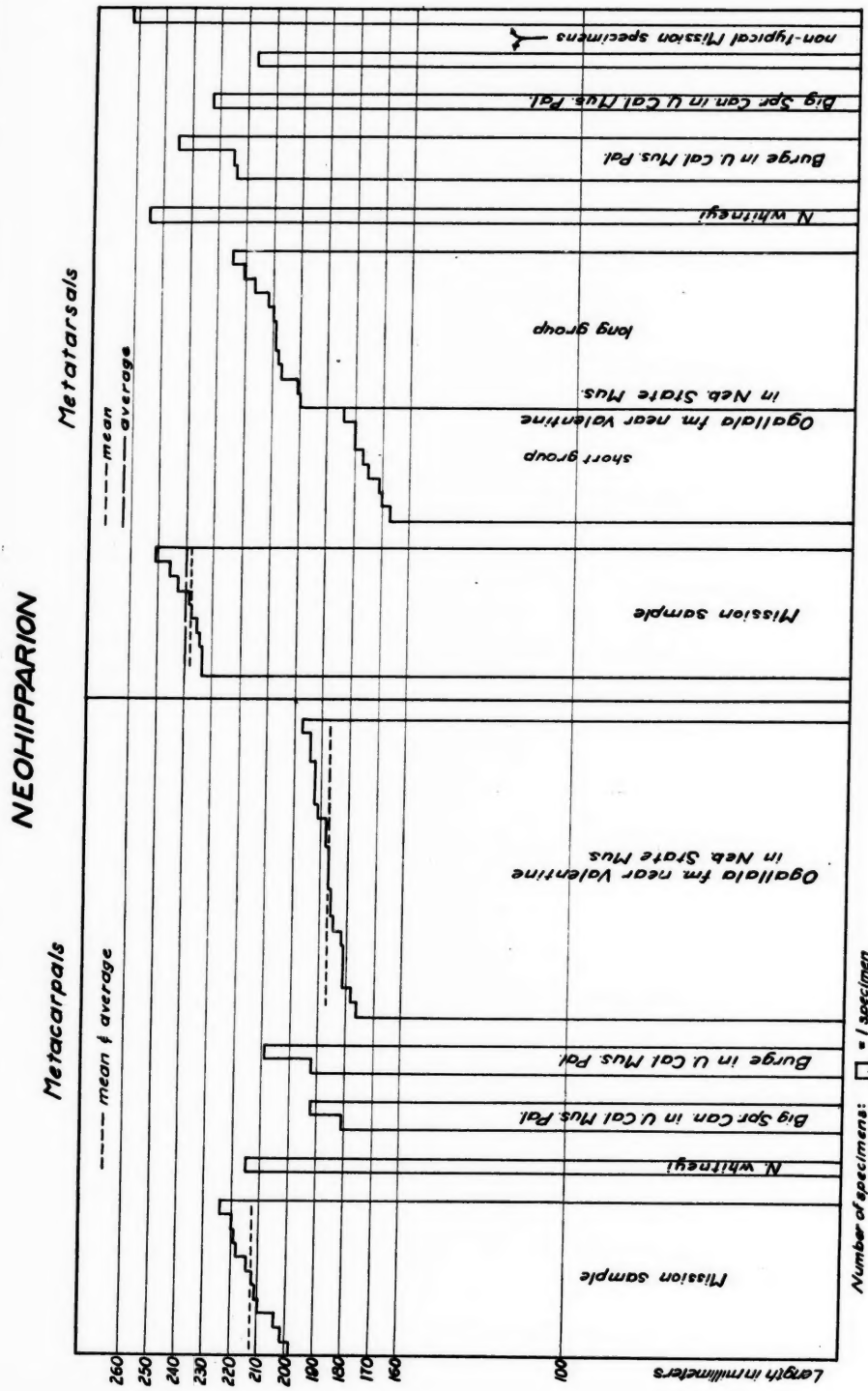
The two non-conforming metatarsals (53189) may be referable to *Neohipparion* but they are well out of the range of the above specimens. The smallest of these is 217.5 mm. long and relatively much more slender than the others. The splint scars are not developed along the shaft, although the central prominence is at the anterior face of the shaft. This specimen may belong to a species of *Pliohippus* or to a species of *Neohipparion* which cannot be distinguished through the isolated teeth found in this locality.

The other non-conforming metatarsal is 252.0 mm. in length, and it is much more slender than the other specimens. It also lacks the prominent splint scars and the central prominence is pushed well forward. This specimen is 7.0 mm. longer than the type of *N. whitneyi*.

The accompanying chart presents a summary of the measurements of the Mission material and other specimens to which it has been compared. The same information is presented graphically in figure 7.

PLIOHIPPUS sp.

53218 65 upper cheek teeth
53224 Left mandible with P_2-M_3
53225 Right mandible with P_2-M_3



TEXT-FIG. 7—Graphic comparison of lengths of *Neohipparion* sp. metapodials.

VARIATION IN LENGTH OF *Neohipparion* METAPODIALS

	Maximum length	Minimum length	Average length	Difference maximum & minimum length	% of average difference in length
Mission Mtc III (11 specimens)	224.0	199.0	212.04	23.0	11.2
NSM Mtc III (21 specimens)	196.8	175.7	187.2	21.1	11.2
Mission Mtt III (9 specimens)	252.0	233.5	239.6	18.5	7.7
NSM small Mtt III (8 specimens)	184.3	166.9	176.5	17.4	9.9
NSM large Mtt III (11 specimens)	229.4	200.4	211.0	25.0	11.3

53226 Left mandible with P_3-M_2
53227 Symphysis with right mandible and P_{2-3}
53242 Fragment of mandible with P_2
53243 Right maxillary with dP^4-M^3
53224 59 lower cheek teeth
566 Left mandible with P_{2-4}
55219 Right maxillary with P^3-M^1
576 Left mandible with P_2–M_3
5711 13 upper cheek teeth
5712 5 lower cheek teeth

Gregory's (1942) excellent review of the status of early Pliocene *Pliohippus* covers the problems of specific determination among the known forms. The available teeth vary greatly in size and shape; protocones range from oval to rounded, folds on the fossettes vary from simple single inner folds to several complicated folds; in general the smaller teeth in the sample have simpler fossette borders and may represent a separate species; the cement covering varies from very light to quite heavy.

Although the largest specimens are larger than those from Big Spring Canyon that Gregory (1942) referred to *P.* cf. *pernix* and the specimens from the Burge that he referred to *P. supremus*, I hesitate to refer this material to any other species or to exclude the possibility that it may be referable to either of these species.

PLIOHIPPUS cf. MARTINI

53221 An isolated upper cheek tooth.

A single upper cheek tooth may be referable to *Pliohippus martini* (Hesse) from the Ogallala Cragin Quarry in Beaver County, Oklahoma.

This tooth has an antero-posterior diameter of 15.5 mm. and is 16.5 mm. in transverse diameter, the remaining crown height is 24.5 mm. along the mesostyle. The crown is moderately curved; the parastyle and mesostyle are narrow, flaring near the base of the crown; the fossettes are simple with a single minor inflection on the posterior end of the lingual border of the prefossette; the protoloph is slightly pinched-in at the junction with the protocone; and the post-protoconule groove is widely open.

The teeth which Green (1956) referred to *P. martini* from the Wolf Creek area have complicated fossette borders and a pli-caballin fold; all of these variations may be seen in the type of this species.

NANNIPPUS cf. GRATUS

53190 7 metatarsal III's
53191 4 metacarpal III's
53194 A metacarpal III
53216–53246 191 lower cheek teeth
53219 165 upper cheek teeth
53228 Fragment of ramus with dP_{2-4}, M_1, and the alveolus for dP_1
53230 Fragment of ramus with I_2–P_4
53231 Fragment of ramus with I_3–P_3
53233 Fragment of ramus with P_{2-4}
53235 Fragment of ramus with Canine and P_2
53236 Fragment of ramus with dP_{2-3}
53237 Fragment of ramus with P_{2-4} and the alveolus for P_1
53238 Fragment of ramus with P_3–M_1
53240 Fragment of ramus with P_{2-4}
53241 Fragment of ramus with P_{2-4}
53246 Fragment of ramus with dP_{3-4}
5510 Fragment of ramus with P_{3-4}

The above list indicates that *Nannippus* is an extremely abundant form in this fauna. Undoubtedly there were many fairly complete skulls in the deposit that were destroyed during the operation of the sand pit.

Sixty-five of the isolated cheek teeth were selected for measurement by Miss Axsell (see page 970). This group did not include P_2's, M_3's, unworn, heavily worn, or milk teeth. This sample varied as follows:

	Smallest	Largest	Average
Greatest antero-posterior diameter of crown	12.0	21.8	17.2
Greatest transverse diameter of crown	12.0	18.3	15.01
Ratio of antero-posterior diameter of crown to transverse diameter	.67	1.20	.876
Antero-posterior diameter of protocone	4.4	7.7	6.04
Transverse diameter of protocone	1.7	3.9	2.85
Ratio of antero-posterior diameter of protocone to transverse diameter	.26	.71	.485

As within any large collection of isolated horse teeth, there is a wide variation among these specimens. Characters that are often used as specific indicators and which show a great deal of variation within this sample include: gross size, size ratios (i.e., ratio of antero-posterior diameter to transverse diameter of the crown and the protocone), shape and size of the protocone, and degree of complication of the fossette borders.

A few noteworthy variations found in this sample include:

1) Twenty specimens have partially or moderately open hypoconal grooves, while the remainder are closed to form hypoconal fossettes.
2) Forty-seven have a spur on the anterior end of the protocone.
3) One hundred have a pli-caballin fold and a few have double pli-caballin folds.

The variation within this sample suggests that extreme care should be taken in assigning specific designations to isolated horse teeth. Both *N. retrusus* (Cope) and *N. gratus* (Leidy) are characterized by a hypoconal fossette (Stirton, 1940, p. 186), yet approximately 12% of this sample has an open groove. This again serves to point up the fact that primitive (or advanced) characteristics may be present in certain individuals within any population.

Similar variations may be seen in the 191 isolated lower cheek teeth and the 15 fragmentary rami from this locality. Parastylids may be either connected or isolated, and in many teeth the parastylid is represented by several isolated pillars. The P_3 of one jaw (5510) has five isolated pillars in the position of the parastylid. Those teeth that do have isolated parastylids appear to be premolars.

Only eleven metapodials (53190 and 53191) may be definitely referred to this genus. Another metacarpal (53194) may also be referred to *Nannippus*, but it is somewhat longer than the other specimens in this small sample. The measurements of these elements are shown in the accompanying table:

Nannippus cf. *gratus* METAPODIALS

	Length	Transverse Diameter at Proximal End	Transverse Diameter at Colateral Process	Transverse Diameter at Distal End
Metatarsals				
(53190)	162.5	21.0	20.2	19.6
	164.5	19.3	18.7	18.5
	165.0	20.7	19.0	18.8
	165.0	21.1	21.1	19.4
	167.0	21.5	20.3	18.5
	167.0	21.6	20.8	19.4
	170.0	20.5	19.1	17.5
Metacarpals				
(53191)	141.0			
	144.0	22.7	21.5	20.8
	146.0			
	146.0		20.3	19.5
(53194)	156.0	23.2	22.0	22.4

TAPIRIDAE

TAPIRUS sp.

Text-fig. 8

53270 Fragment of right ramus with two cheek teeth.

A jaw fragment with two cheek teeth was presented to the Museum of Geology by the late G. B. Zeitner of Mission, South Dakota. Although *Tapirus* is well known from the early Pliocene localities of the Great Plains and from the Truckee formation in Western Nevada, its presence seems to be a well kept secret as far as the literature is concerned. Until the scattered specimens that are tucked away in various collections are brought together and studied, specimens such as this must remain specifically indeterminate and serve only as an indication of the geographic and geologic range of the genus.

RHINOCEROTIDAE

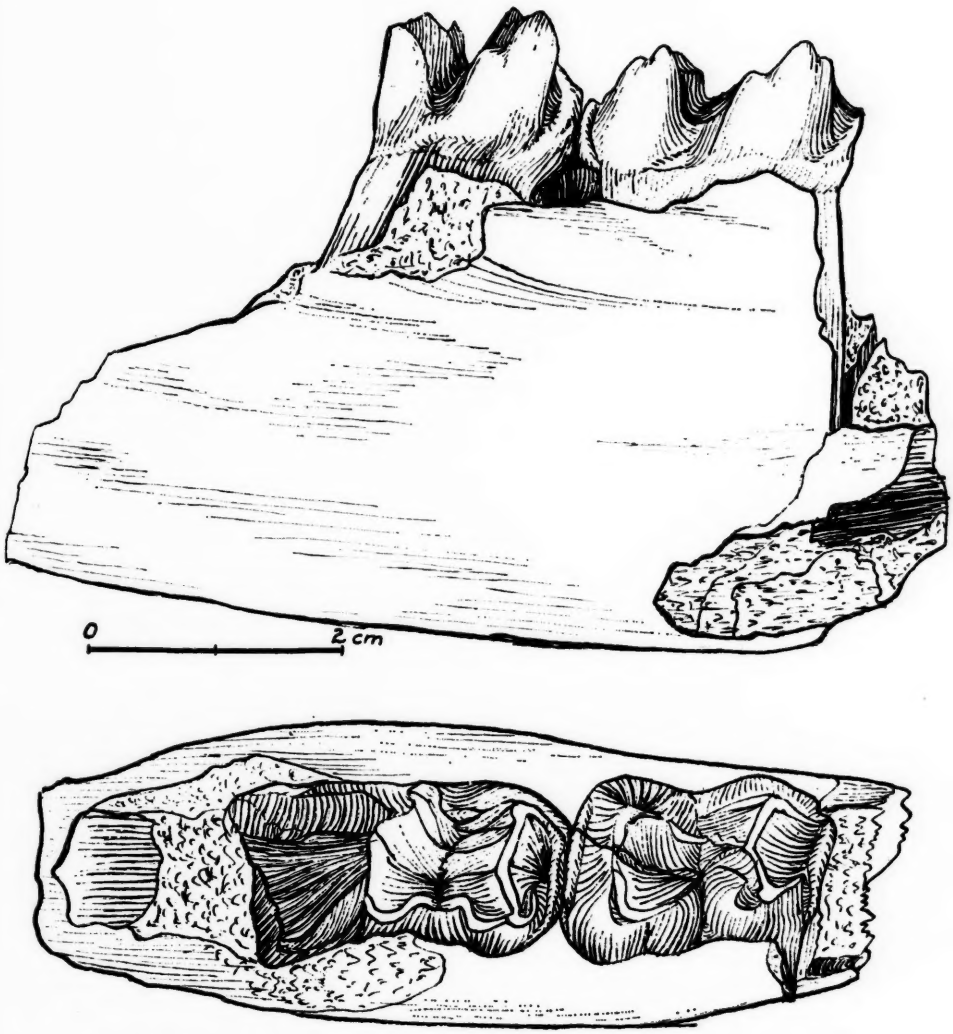
TELEOCERAS cf. FOSSIGER

53185 10 isolated upper cheek teeth
53186 5 isolated upper cheek teeth
53206 Large lower cheek tooth
53207 Fragment of right mandible with P_4 and alveoli of M_1
53208 Right mandible and symphysis with tusks, P_4-M_3, and alveoli for P_3
53209 Fragment of left mandible with P_4-M_3
53210 Fragment of right mandible with M_{2-3} and broken M_1
53211 Fragment of right mandible with P_{3-4}, broken tusk, and root of P_2
53213 Juvenile cranium with P_{2-3}, unerupted P_4, and alveoli for remainder of teeth
53214 Adult cranium with P^2-M^3
53215 Tibia
53216 2 metapodials
53271 Symphysis with I_3, P_2, and alveoli for I_{1-2}
5511 Fragment of left mandible with P_{2-3}
5515 Fragment of right mandible with P_4-M_3
5713 Partial jaw with symphysis, P_{2-4}, and unerupted M_1
5719 Fragment of right mandible with M_2, broken M_1 and M_3, and alveolus for P_4
5723 Astragalus
5724 Miscellaneous foot elements
592 Fragment left mandible with symphysis and P_{2-4}

It seems to be traditional to refer all medium size specimens of *Teleoceras* from the early Pliocene of North America to *T. fossiger* Cope. Each author acknowledges the fact that the genus needs a complete revision and that there are probably several unrecognized species lurking under the guise of *T. fossiger*. As the material from the Mission sand pit is not an adequate basis for the beginning of such a revision, I will also assume the "Let someone else do it" attitude and questionably refer this material to that already overloaded species.

A fine cranium (53214) was collected in small pieces by Mr. Roman Welfl of the South Dakota Highway Department after being excavated by Mr. Gus Schultz of the Summit Construction Company with a D8 bulldozer. Skillful reassembly by Dr. Morton Green has produced an excellent specimen with nearly complete dentition. The M^3's are moderately worn; the protocone is broad at the base and partially isolated by opposing sulci; the antecrochet is broadly rounded; the metaloph is broad with a strong crochet which, on the left side, nearly isolates the prefossette, although it would not become an isolated lake until the very last stages of wear; the very faint parastyle folds would disappear with slightly more wear; the cingulum is very weakly developed across the end of the protoloph, a small cingulum extends vertically along the end of the metaloph, near the base of the loph it swings labially for a short distance and then continues vertically to the base of the tooth. The M^2's are worn nearly to the base of the lophs; the protocone is broadly rounded and nearly separated from the remainder of the protoloph by deep sulci; the antecrochet is strongly developed and extends posterad of the base of the crochet so that the central valley is shaped like a "?"; a small ridge in the floor of the central valley extends lingually from the base of the antecrochet to within a short distance of the edge of the crown; the post-fossette is isolated. M^1 is worn to the point where the fossettes are isolated lakes. P^4 is heavily worn; the fossettes are isolated; the cingulum is well developed as a ridge connecting the base of the protocone with the hypocone. P^3 and P^2 are similar to P^4 except in size and proportion. P^1 is missing, although an alveolus on the right maxillary may have held a small anterior cheek tooth. The top of the nasals has a well developed rugosity for the base of the horn.

A partial cranium (53213) of a juvenile has very thin and smooth nasals. As M^1 is partially erupted, this cranium may either be that of a female or the horn may not de-



TEXT-FIG. 8—*Tapirus* sp. SDSM 53270, fragment of right mandible. ×1.75.

velop until the individual is approaching full maturity.

The lower dentitions are either heavily worn or fragmentary. Of particular interest is a jaw fragment and symphysis (53271) of a very young individual. This specimen has a nearly unworn dP_1 which is three lobed and tapers anteriorly to a point, although just below the crown the anterior face becomes flattened; the posterior lobe contains a rather large fossette and is separated from the median lobe by labial and lingual grooves, the latter is the most prominent as the posterior lobe expands lingually; the anterior lobe is prominently separated from the median lobe by deep grooves which originated above the center of the anterior root. The dP_1 and the dC are separated by a long diastema with a wide labial concavity that narrows the symphysis so that the sides of the rami are nearly parallel; the anterior edge of the symphysis is widely truncated. The dC is located at the anterolabial corner of the jaw which tapers toward the midline.

The dC is procumbent; mushroom shaped in plan view with the greatest flare toward the midline; a transverse groove divides the crown into equal halves. The small alveolus for the ?dI_3 is close to the dC and near the lingual edge of the symphysis. Between the dC and the midline is an elongate double alveolus which opens diagonally into the end of the symphysis; this alveolus contains two teeth; the smaller is needle-like, it is either the dI_2 or I_2; the dI_1 or I_1 is larger, with a rounded featureless crown resembling the head of a wooden match.

Taken by itself this material adds little to our knowledge of this genus. In the future when the North American late Tertiary Rhinoceroses are completely reviewed, this collection should form an integral part of such a study.

ARTIODACTYLA
TAYASSUIDAE
PROSTHENNOPS sp.

53272	Isolated Canine
53273	Maxillary fragment with M^{1-2}
53274	Fragment of mandible with M_{1-2}
54302	Fragment of mandible with P_3–M_3 and alveoli for Canine and P_2
54359	Fragment of mandible with P_4-M_1
55215	Fragment of maxillary with M^{1-2}
5683	Fragment of mandible with P_3-M_3
5684	Fragment of mandible with P_3-M_3 and alveoli for P_2, this is probably the right side of 5683.

Although there is considerable variation within this suite of specimens, it is evident that they represent a single species.

Two partial mandibles (5683 and 5684) which appear to belong to the same individual contain teeth that are essentially unworn. The alveoli of P_2 indicate that this tooth was small and narrow with the posterior root very little larger than the anterior. P_3 has a transverse anterior cingular cusp; two equal and opposite central cusps; and two opposite posterior cusps; the sides of the tooth are nearly parallel with a slight anterior taper. The P_3 of 54302 is slightly smaller with a sharper taper. P_4 has a very small anterior cingular cusp at the labial corner; paired opposite principal cusps with anterior and lingually extending spurs that join the cingulum at the anterior lingual corner; a small cusp on the midline is tightly appressed to the principal cusps and joins a similar cusp posteriorly to fill the transverse medial valley; the posterior moiety of the tooth consists of four tightly appressed cusps, the anterior of these is on the midline and appressed to the midline cusp anterad, posterad to this cusp is a transverse pair of cusps; the crown ends posteriorly with a single medial cusp. M_1 is the only tooth with extensive wear; its pattern is similar to that of P_4 with the exception that the posterior end of the crown is formed by a transverse pair of cusps. M_2 is the largest tooth in the lower cheek tooth series; it is similar to M_1 except that posteriorly there is a moderately large medial cusp and two small lateral cusps. M_3 is similar to M_2 in crown pattern except that it is elongated and the posterior cusps form a talonid, the medial anterior cusp is divided into two cuspules by a faint lateral pinching, the cingulum forms a small circular cusp on the labial side of the transverse valley. The talonid of the M_3 of 54302 is somewhat narrower than that of 5684.

The crown pattern of the upper cheek teeth is seen in 53273 and 55215. P^4 has the anterior moiety worn into a deep basin; the posterior portion is formed by three transverse cusps, the labial is the largest, the medial is laterally compressed, and the lingual is rounded and slightly smaller than the labial; there is a broad posterior cingulum on the labial cusps. M^1 has an anterior, labial, and lingual cingulum; an anterior medial cingular cusp; paired transverse anterior cusps; a small medial cusp attached to the posterior paired transverse cusps; paired transverse cusps; and a posterior medial cusp that is slightly linguad of the midline. M^2 is similar to M^1 except that it is larger and relatively broader; the posterior cingular cusp is absent as the cingulum sweeps upward and merges with the lingual posterior cusp.

In spite of the seemingly adequate amount of material available, it is not possible to make a specific determination for these specimens. The premolars suggest that this form is advanced over the older forms from this region, *P. xiphodonticus* Barbour (1925) and *P. niobrarensis* Colbert (1935). Colbert (1938) pointed out that the teeth of the various species of *Prosthennops* are very similar, which makes specific deter-

minations on teeth alone very difficult. On the basis of the material at hand, an identification beyond the generic level is not acceptable.

MERYCOIDODONTIDAE

USTATOCHOERUS sp.

53266 Fragment of left maxillary with Canine, P^1, and P^{3-4}
53267 Fragment of left mandible with P_2 and P_4
53268 2 isolated upper cheek teeth
53269 1 isolated upper cheek tooth
554 Fragment of right maxillary with P^1-M^1

On the basis of size and geologic position the above material is referred to *Ustatochoerus*. The crown pattern of the P^3 in 53266 suggest that this form may be *U. skinneri* Schultz and Falkenbach (1941).

CAMELIDAE

Immature ?PROTOLABIS sp.

53260 Fragment of mandible with roots of dP_2 and slightly worn dP_3

This small and delicate jaw fragment is broken anterad of the mental foramen and posterad through the alveolus for the anterior root of the dP_4. There is no indication of the presence of a tooth above or posterior to the mental foramen which indicates that there is no dP_1 or that it is not in its usual position. Gregory (1942, p. 398 and figure 35b) indicates that the immature ?*Protolabis* from Big Spring Canyon is also lacking a dP_1. The dP_2 is represented by two small roots. The dP_3 is three lobed with a lake in the posterior lobe; this tooth resembles the P_4 in adult camels and the dP_3 in SDSM 52508 which is discussed below under "Immature *Procamelus* or *Pliauchenia*." All of these characteristics may be found in the specimen (UCMP 32309) from Big Spring Canyon that Gregory (1942, p. 397–400) discussed in his monograph on that fauna.

PROCAMELUS GRANDIS Gregory

53252 Left ramus with P_{1-2}, P_4-M_3, and roots of P_3
53254 Left ramus with P_{1-2}, P_4-M_3, and roots of P_3
53255 Left ramus with P_4-M_1
53256 (?) Symphysis with I_2—Canine and alveoli for I_1 and I_3
53257 Fragment of right ramus with P_{2-4}
53259 (?) Fragment of left ramus with P_3
555 Left ramus with P_1-M_2
5513 Fragment of right maxillary with P^2-M^1
5514 Fragment of left maxillary with P^3-M^3
55214 (?) Fragment of left ramus with P_3

This abundant material displays the same variations that are found in the type and topotypal material from Big Spring Canyon. The two more complete rami (53252 and 555) and a fragment (53254) have moderately worn dentitions that closely resemble the type specimen. The two maxillary fragments (5513 and 5514) are not significant although it should be noted that the P^2 of specimen 5513 is similar to the paratype (UCMP 33449) and that the P^3 has a well developed posterior re-entrant that does not appear in any of the Berkeley or Rapid City collections from the type locality at Big Spring Canyon, South Dakota.

PROCAMELUS FOXI[4] Macdonald n. sp.

Text-fig. 9

Type.—Right ramus and symphysis with Canine, P_3–M_3 and roots or alveoli of I_{1-3} and P_{1-2}. SDSM 53251.

Type Locality.—Mission Quarry. V5314.

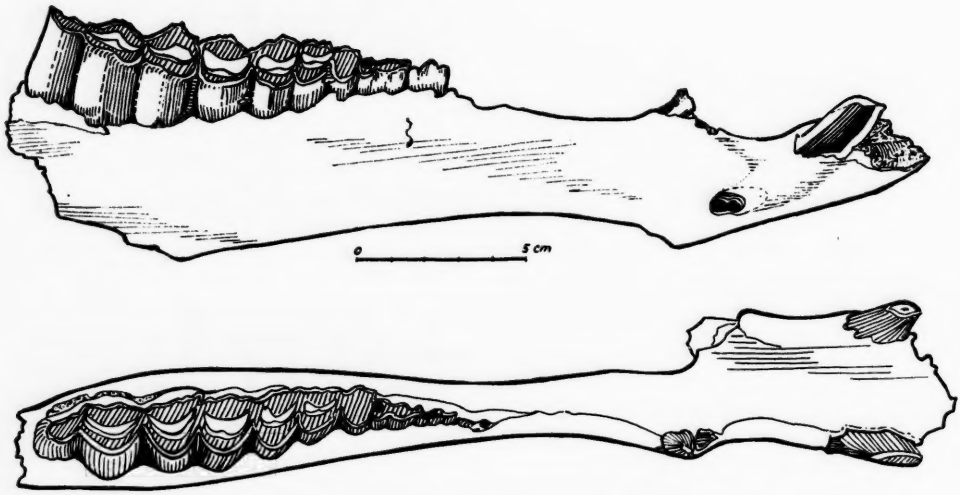
Age.—Clarendonian—Early Pliocene.

Fauna.—Mission.

Diagnosis.—P_1 double rooted, long diastema between P_1 and P_2, P_3 three cusped without re-entrant, P_4 with re-entrant opening at lingual posterior corner.

Description.—Ramus slender and shallow; downcurved between anterior end of cheek tooth row and posterior end of symphysis below anterior root of P_1; large elongated mental foramen below diastema between Canine and P_1. M_{1-3} as in other species of *Procamelus;* posterior lobe of M_3 more rounded and not offset as abruptly as in *P. grandis* Gregory. P_4 distinctly three lobed with small re-entrant in posterior lobe opening at posterior-lingual corner of tooth. P_3 greatly reduced, three cusped with primary cusp and smaller anterior and posterior cusps. P_2 alveoli only; two rooted; smaller than P_3. P_1 roots only; separated from P_2 by long diastema; very large as judged from the roots. Canine large; separated from P_1 by diastema nearly half the length of the diastema between P_1 and P_2. Incisors represented by roots and alveoli only; increase in size from I_1–I_3; alveoli separated by small septa of bone.

[4] For the late Mr. Thomas Fox, former owner of the Mission sandpit.



TEXT-FIG. 9—*Procamelus foxi* Macdonald n. sp. Type specimen, SDSM 53251, right ramus. ×0.46.

Discussion.—This species with its massive double rooted P_1, the long diastema between P_1 and P_2, and the three lobed P_3 is easily distinguished from the other members of this genus.

The double rooted P_1 is considered to be a primitive feature, as is the simple P_3. The downward break of the ramus in front of the cheek teeth and the long diastema between P_1 and P_2 may represent a specialization or a case of random fixation.

Immature PROCAMELUS or PLIAUCHENIA

53262 Fragment of ramus with dP_4
53508 Fragment of ramus with dP_{3-4}

These two specimens may be referable to either *Procamelus* or *Pliauchenia*. The dP_3 is three lobed with the lobes increasing in size posteriorly, the posterior lobe has a small lake which parallels the midline on the lingual side. The dP_4's are sub-equal, with that of 53262 being somewhat more massive.

dP_3 is similar to the P_4 of *Procamelus foxi* in that the anterior lobe is well rounded but the center lobe is laterally compressed and the posterior lobe is relatively larger. This tooth is larger and narrower than the P_4 of *P. foxi* and much narrower and shorter than the P_4 of *P. grandis*. Similarly, it is relatively narrower although nearly as long as the P_4 in the jaw (53263) which is herein tentatively referred to *Pliauchenia magnifontis*.

PLIAUCHENIA cf. MAGNIFONTIS

53258 Fragment of right ramus with P_{1-2}
53253 Fragment of right ramus with P_1–M_2

These two specimens are questionably referred to *P. magnifontis* Gregory (1939). The more complete specimen (53253) has moderately worn dentition and a small unworn P_1 which may be in the process of erupting. There is a single small alveolus in front of the P_3 and separated from it by a short diastema. This alveolus may have held either P_2 or dP_2. The presence of this alveolus and the generally lighter construction of the jaw suggests that it is not a variant of *Procamelus grandis* but is referable to *Pliauchania magnifontis* from the Big Spring Canyon fauna. The second specimen (53258) is a small fragment with a small P_1 and a double rooted P_2 or dP_2 which has been pushed out of the ramus. This tooth is so situated that early loss is certainly indicated.

PARACAMELUS or AEPYCAMELUS sp.

53250 Distal end of a metapodial
53261 Upper cheek tooth

These fragments are our only indication that giant camels lived in this area at the time of deposition. These remains may be referable to either *Paracamelus* or *Aepycamelus*.

The tooth is moderately worn and meas-

ures 44.1 mm. antero-posteriorly at its greatest diameter and 35.5 mm. transversely near the base of the enamel. The metapodial is 52.0 mm. transversely and approximately 57.0 mm. antero-posteriorly at the distal end.

ANTILOCAPRIDAE

COSORYX sp.

53281	Fragment of deeply grooved horncore with heavy fork
53283	Distal and proximal ends of a metacarpal.
53284	Fragment of left ramus with M_{2-3}
53496	Fragment of horncore with base and partial fork
53497	Fragment of horncore with base of shaft and burr
53498	Fragment of horncore with section of shaft without burr
53499	Fragment of horncore with section of shaft and burr
53502	Fragment of horncore with small fork
53503	Fragment of horncore with medium flattened fork
53504	Fragment of horncore with base of shaft and medium fork, without burr
53510	Fragment of right ramus with $?M_2$
54303	Fragment of left ramus with P_4–M_3
557	Fragment of horncore with medium flattened fork
558	Fragment of horncore with burr and fork
5516	Distal end of tibia
55184	Fragment of left ramus with dP_4
5648	Fragment of horncore with flattened fork
5680	A metatarsal
5716	Fragment of horncore with fork

The jaw fragments are similar in size and shape to those from Big Spring Canyon and are presumably referable to the same species. Twelve fragmentary horncores are also referable to the same species. Three of these have "burrs," three, with the lower part of the shaft preserved, do not have "burrs," and the remainder are only forks or tines. Two specimens (53504 and 558) are the same size, the diameters of the shaft being approximately the same and the length of the shaft about the same; one of these (53504) is smooth surfaced and does not have a burr, the other (558) is burred and moderately ruggose.

Is it possible that the presence or absence of a "burr" could be a secondary sex characteristic? About 60% of the Recent *Antilocapra* females have horns which are generally small; it is possible that the smooth burrless horncores of *Cosoryx* and related genera are those of females who did grow horns.

One core (53281) is heavily lined with a network of grooves which apparently carried the veination for the nourishment of the growing horn sheath. This grooving is progressive with age in the Recent *Antilocapra* and we may presume that the same condition existed in the Pliocene.

Two specimens are complete enough to be measured. 558 is 20 mm. from the base of the horncore to the top of the burr and 91 mm. from the top of the burr to the crotch of the fork. 53504 is without a burr and is 89 mm. from the base of the horncore to the crotch of the fork.

I have referred this material to *Cosoryx* as Mr. Beryl Taylor, of the Frick Laboratory, from whom I requested an opinion, assured me that the Mission specimens were well within the range of variation of materials in the Frick collection, and that these collections contained as yet unpublished material that would substantiate the validity of *Cosoryx*.

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MIOCENE CARNIVORES, TEXAS COASTAL PLAIN

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ABSTRACT—*Daphaenodon* is recognized in Texas for the first time where it is associated with *Amphicyon*. *Amphicyon*, an European genus, spread to North America during late Early Miocene time and is found on the Gulf Coast in rocks so that age to latest Miocene or earliest Pliocene. On the basis of the presently known material, both *A. pontoni* Simpson and *A. longiramus* White can be identified. *Aleurodon francisi* Hay is reconfirmed as belonging to that genus. The presence of *Tomarctus canavus* (Simpson) and *Cynodesmus iamonensis* (Sellards) is recognized, which extends the range of these species from Florida to the Texas Coastal Plain. *Edaphocyon pointblankensis n. gen. et n. sp.*, a procyonid of close relationship to *Bassariscus*, is described.

INTRODUCTION

A FORTUITOUS combination of interfingering fossiliferous marine and fossiliferous nonmarine beds and simple structure on the Texas Coastal Plain should eventually make possible accurate correlation of the continental sequence of formations of the interior of North America and the marine sequence of the margin. Although much of the Tertiary sequence at the surface on the Texas Coastal Plain is of continental origin, only the Miocene, Pliocene, and Pleistocene have produced mammalian fossils, the most useful for Tertiary correlation. There is still much careful descriptive work necessary before the faunas are completely described.

Quinn (1952, 1955) and Wilson (1956, 1957) have discussed the stratigraphic sequence of the Texas Gulf Miocene and Pliocene formations and their several biostratigraphic units. The latter are the Garvin Gulley fauna (late Arikareean), the Burkeville fauna (early Hemingfordian), the Cold Spring fauna (middle Hemingfordian), and the Lapara Creek fauna (late Barstovian). Substantiation for this sequence has been furnished by Quinn (1955) in his description of some groups of horses and in part by Wilson (1957) in his description of the enteledonts.

The present paper deals with the carnivores. Correlations based on these forms do not call for any change in the original sequence of faunas as set up by Quinn (1955), in fact they add further verification. Reports on other mammalian groups will follow as they are ready. The carnivores are a group by which correlations with the European section may be attempted. Tentative correlations are proposed herein.

I am grateful to members of the staffs of Carnegie Museum, Pittsburgh; Department of Paleontology, University of California; Florida State Geological Survey; and Department of Geology and Museum of the Agricultural and Mechanical College of Texas for the loan of material or furnishing casts of important specimens. Casts of European amphicyonid material was most generously furnished by Professor Richard Dehm of Munich and Professor Jean Viret of Lyon. The University of Texas Research Institute and the Geology Foundation of The University of Texas provided financial assistance. The American Philosophical Society generously defrayed the cost of visiting meseums in Europe.

The following abbreviations are used to refer to various institutions: A.M.N.H., American Museum of Natural History, New York; B.E.G., Bureau of Economic Geology, The University of Texas, Austin; B.M., Naturhistorische Museum, Basel, Switzerland; C.M., Carnegie Museum, Pittsburgh; C.N.H.M., Chicago Natural History Museum, Chicago; I.P.H.G., Institut für Paleontologie und Historische Geologie, Munich, Germany; M.C.Z., Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; T.A.M., Agricultural and Mechanical College of Texas, College Station; U.C., University of California, Berkeley; U.L., Laboratorie de Geologie, Université de Lyons.

GARVIN GULLEY FAUNA[1]

Family CANIDAE
Subfamily AMPHICYONINAE
DAPHAENODON cf. SUPERBUS
Peterson, 1909
Text-fig. 1a

The Oakville formation from the Cedar Run locality of Wood and Wood (1937) has yielded a tooth (B.E.G. 40068-15) which by comparison with a cast of the type, C.M. 1589, is approximately the same size as the M^2 of *Daphaenodon superbus* Peterson (1910, pl. 75). On the Cedar Run specimen the paracone is larger than the metacone, which accentuates the turned-up antero-external corner of the tooth or the broken-backed condition. The external cingulum is prominent. The protoconal ridge rises gradually to the center of the tooth with no proto- or metaconules visible. Internal to the protoconal ridge is a very broad cingular platform. The former presence of a low hypocone is indicated by a more heavily worn area.

AMPHICYON LONGIRAMUS White, 1942
Text-fig. 1b–l

Amphicyonid material from Garvin Gulley in the collection of Texas A. & M. College has been catalogued under the number 2635. The material is fragmentary and does not belong to a single individual. It is therefore risky to assign it to a particular species, but for reasons given below it is identified as *A. longiramus* White. An incomplete M_1, (T.A.M. 2635, text-fig. 1b) is, by comparison with the type, very close to *A. longiramus* White. Fragments of P^4, M^1, M^2, M^3, $\underline{C}$, and $\overline{C}$—all catalogued as T.A.M. 2635—are of equal robustness and of similar structure to referred specimens of *A. longiramus* White in the collections at the Florida Geological Survey and the Museum of Comparative Zoology, Harvard University.

A complete right M^1 (T.A.M. 2635, text-fig. 1c) is more like the M^1 in *A. riggsi* McGrew. It is more triangular than *A. longiramus* White of the Thomas Farm but this may be individual variation. The paracone is one-third larger than the metacone. On the anterior side of the paracone, the cingulum rises to a point but is reduced to absent externally. Posteriorly, a faint cingulum rises to a point on the posterior side of the metacone. The tooth as a whole is triangular but slightly bent posteriorly. The protocone is very prominent and located anterointernally to the center of the tooth. A low metaconule is faintly visible. The internal cingulum is well developed as a ridge but without a hypocone. Its strongest expression is on the postero-internal flank of the tooth.

A fragment of a left M^1 (T.A.M. 2635, text-fig. 1d) is larger than the right and is indistinguishable from comparable teeth of *A. longiramus* from Thomas Farm. The left M^1 measures 19.2 mm. antero-posteriorly across the protocone, whereas the right M^1 measures only 16.0 at the same position. The cingulum on the fragmentary left M^1 is considerably broader than that of the right M^1. An M^2 (text-fig. 1e) bearing the same number and from the same place has the swollen appearance caused by the broad internal cingulum and the low, rounded,

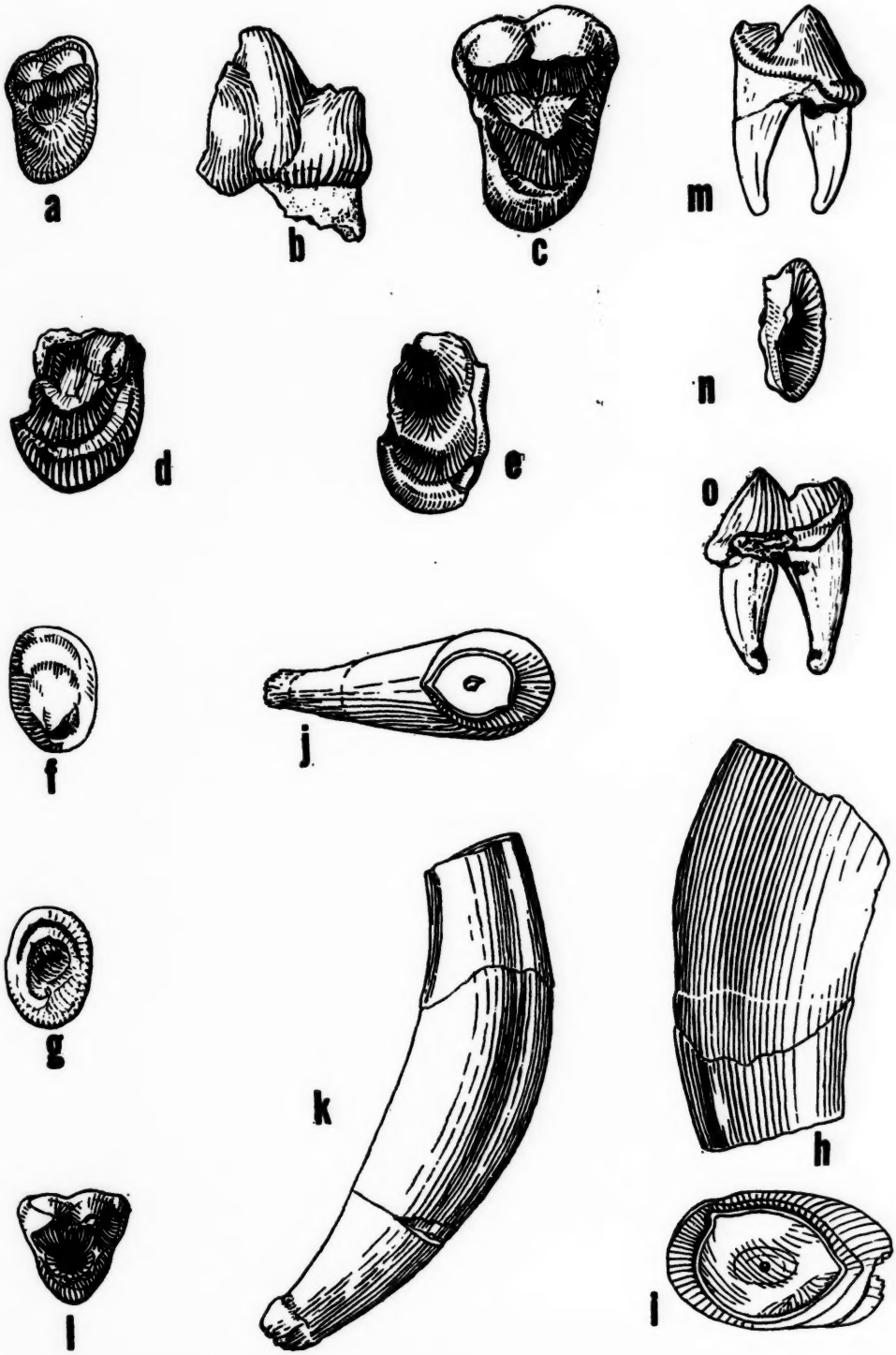
[1] Oakville fauna of Quinn (1952).

TEXT-FIG. *1*—All specimens from Garvin Gulley fauna
All figures ×1

a—Daphaenodon cf. *superbus* Peterson. M^2, B.E.G. 40068-15, Cedar Run locality, Washington County, Texas.

b-l—Amphicyon longiramus White. All from Garvin Gulley locality, Grimes County, Texas. *b*, M_1, T.A.M. 2635. *c*, M^1, T.A.M. 2635. *d*, M^1, T.A.M. 2635. *e*, M^2, T.A.M. 2635. *f*, M^3, T.A.M. 2635. *g*, M3, U.C. 32611. *h,i, C*, T.A.M. 2635, external and ventral views. *j,k*, $\overline{C}$, T.A.M. 2635, external and dorsal views. *l*, dM^3, U.C. 32611.

m–o—Amphicyon longiramus White dP^4 or *A. pontoni* Simpson P^4. Garvin Gulley locality, Grimes County, Texas. T.A.M. 2635.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centrally placed protocone. This tooth does not have the posterior bend characteristic of the M^1 and M^2 of the Florida specimens.

An M^3 (text-fig. 1f) with the same number and from the same place is button-like, with paracone and metacone reduced to a low featureless ridge oriented obliquely to the long axis of the tooth. The center of the tooth is dished by wear, but the dished-out portion is rimmed by a low ridge on three sides representing the protocone and proto- and metaconules, although none of these forms a distinct cusp. Internally the cingulum forms a rounded border. This tooth has a broad but bifurcate root.

An M^3 (U.C. 32611, text-fig. 1g) is slightly smaller than its counterpart in the Texas A. & M. College collection. It shows the same pattern on the crown, is a little more worn, and is completely single rooted, a character which is probably of no significance.

In the Texas A. & M. College collection there are three fragments of canines, all bearing the number 2635. One (text-fig. 1h,i) is an upper, the others, only one of which is figured (text-fig. 1j,k), lowers. The upper canine is inflated dorsal to the upper margin of the enamel. There is a sharp ridge at the posterior margin and another at the antero-internal margin.

A left dM^3 of *Amphicyon* (U.C. 32611, text-fig. 11) is a triangular tooth. The paracone is only slightly larger than the metacone. A faint cingulum extends across the external side of the tooth and projects both anteriorly and posteriorly to make prominent cingular shelves at both the antero- and postero-external corners. There is no cingulum internal to the protocone.

AMPHICYON indet.
Text-figs. 1m–o

An upper carnassial (T.A.M. 2635, text-fig. 1m,n,o) is either a deciduous tooth of *A. longiramus* or belongs to *A. pontoni* Simpson, since it is proportionally small when compared to the permanent molars of *A. longiramus*. The anterior ridge on the paracone is not slanted posteriorly as much as in *A. riggsi* (McGrew, 1939) but is directed more straight up and down, as in *A. americanus* (Wortman, 1901). The protocone is broken off but its place of attachment to the main body of the tooth is apparent. The protoconal base originates 3 mm. posterior to the anterior edge of the tooth so that the protocone itself must have been approximately opposite the paracone.

Subfamily CANINAE
CYNODESMUS IAMONENSIS
(Sellards), 1916
TEPHROCYON SCITULUS Hay, 1924

Nothing can be added to Hay's (1924) description of *Tephrocyon scitulus*. The specimen now bears the number 2380 in the collection of Texas A. & M. College Museum. Since Olsen (1956) has given a more detailed analysis of *Cynodesmus iamonensis* (Sellards, 1916), it is obvious that *Tephrocyon scitulus* Hay is synonymous with *Cynodesmus iamonensis* (Sellards).

BURKEVILLE FAUNA
Subfamily CANINAE
TOMARCTUS CANAVUS (Simpson) 1932
Text-fig. 2a,b,c

A fragmentary right ramus of a lower jaw (B.E.G. 31190-67) from near Pointblank,

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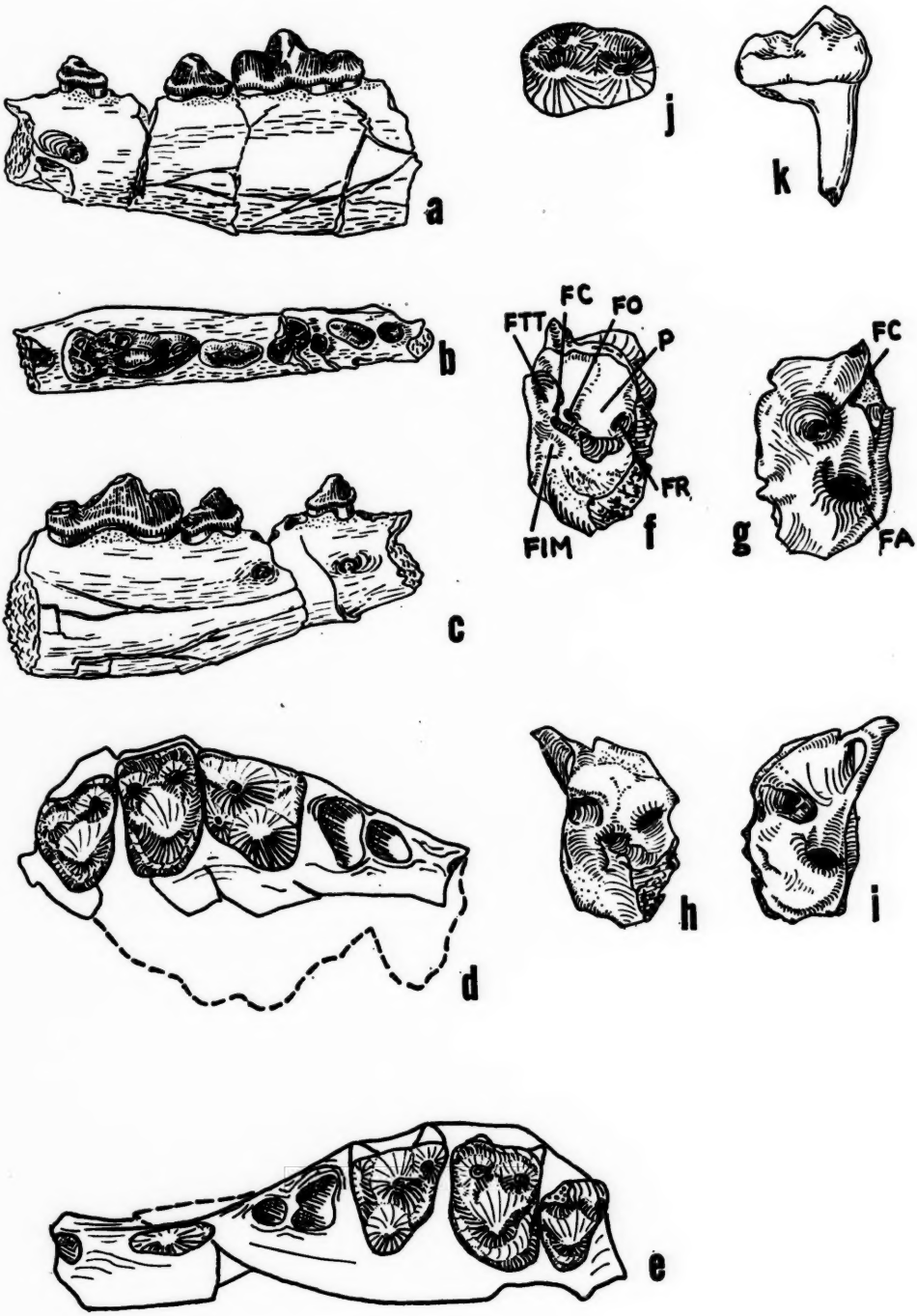
TEXT-FIG. 2

a–c—Tomarctus canavus (Simpson). Internal, dorsal, and external views of lower jaw fragment, B.E.G. 31190-67. Burkeville fauna, near Pointblank, San Jacinto County, Texas. ×1.

d–g—Edaphocyon pointblankensis, n. gen. et sp. B.E.G. 31190–76. Burkeville fauna, near Pointblank, Jacinto County, Texas. *d,e*, Right and left maxillary fragments. *f*, External (ventral) view of right petrosal. *g*, Internal (dorsal) view of right petrosal. ×2.

h,i—Bassariscus astutus. Right petrosal. h, External (ventral) view. FC, facial canal. FIM, fossa for incus and maleus. FO, foramen ovale. FR, foramen rotundum. FTT, fossa tensor tympani. *i*, Internal (dorsal) view. FA, appendicular fossa. FC, facial canal. ×2.

j,k—Amphicyon pontoni Simpson. M_2, dorsal and internal views. B.E.G. 40269-1. Cold Spring fauna, near Cold Spring, San Jacinto County, Texas.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San Jacinto County, Texas, is placed tentatively in *Tomarctus canavus*. Unfortunately no lower jaw elements of *Tomarctus* are known in the Garvin Gulley fauna, and no upper jaw elements of the same genus are known in the Burkeville or Cold Spring faunas. The heel of B.E.G. 31190-67 has the cross-ridge between the entoconid and hypoconid.

Family PROCYONIDAE
Subfamily PROCYONINAE
Genus EDAPHOCYON, n. gen.
Species EDAPHOCYON POINTBLANKENSIS, n. sp.
Text-fig. 2d–g

Type.—B.E.G. 31190-76, a left upper dental sequence with P^2, P^4, M^1, M^2; a right upper dental sequence of the same animal with P^4, M^1, M^2; a left petrosal of the same animal, and numerous fragments of the skull.

Occurrence.—Lower part of the Fleming formation, site 1 (records of the Bureau of Economic Geology, The University of Texas), on the Mrs. Ella McMurray farm, C. E. Abbey survey, near Pointblank, San Jacinto County, Texas. More precise locality data on file at the Vertebrate Paleontology Laboratory, Bureau of Economic Geology, The University of Texas. Biostratigraphic unit, Burkeville fauna (Quinn, 1952; Wilson, 1956, 1957).

Description.—The posterior part of the alveolus for the canine is present on the left maxillary. The alveolus for the first premolar shows that it was single rooted. The left P^2 has a faint cingulum on which is a suggestion of an anterior accessory cusp. There is a single posterior cusp. P^3 is not preserved but the alveoli show that it must have been a triangular tooth since the posterior alveolus is very broad and has a median constriction. P^4 is typically procyonid but not quite like any individual genus of the family. It has a prominent anterior cingulum on which there is a well-developed parastyle. The paracone is the largest cusp and is elongate posteriorly toward the metacone. This gives the external part of the tooth a blade-like appearance, although the blade is short. The protocone is large and located slightly posterior to the parastyle and slightly anterior to the paracone. There is no cingulum at the internal base of the protocone. There is a small but well-developed cusp posterior to the protocone.

M^1 is quite dog-like. The para- and metacones are almost of equal size, but the paracone is slightly larger. There is a prominent external cingulum. The protocone forms the apex of a well-developed V slightly internal to the center of the tooth. The wings of the V pass anterior and posterior to the para- and metacone, respectively. Low ridges lead directly internally from the bases of the para- and metacones to intersect the inside of the wings of the V. The internal cingulum is broad and sharp. M^2 is smaller than M^1 and more triangular shaped. There is an internally directed ridge leading from the paracone but not from the metacone. The internal cingulum is developed only at the internal base of the protocone.

Enough fragmentary material is preserved so that considerable detail may be made of the ear region. The external auditory meatus was formed by the tympanic and the squamosal, as shown by a fragment of the tympanic preserving the unbroken edge of the ventral rim of the meatus. Another fragment of the glenoid area shows a suprameatal fossa just posterior to the postglenoid fossa. The petrous portion of the right periotic is almost complete, but the more delicate bulla is not preserved. It is therefore impossible to tell anything about its shape or whether a septum within the bulla was present.

The petrosal (text-fig. 2f,g) that is preserved is from the right side and is shown with the same bone of the same side of *Bassariscus* (text-fig. 2h,i). The promontory (text-fig. 2f,p) is shaped most nearly like that of *Bassariscus*. There is no lip over the foramen ovale. The fossa for the tensor tympani is large and deep. The foramen for the passage of the facial nerve passes dorsal to the fossa for the tensor tympani (fossa musculus major of Hough, 1948a). The foramen continues as a canal for a short distance. It is not possible to be certain but it appears that this canal was not covered ventrally. The canal curves caudo-laterad into a sizable pit that contained the origin of the stapedius muscle. This fossa for the stapedius muscle is larger and deeper than that of either *Bassariscus* or *Nassua* and

more like that of *Procyon*. A short groove leads from this fossa to the foramen ovale.

The internal side of the petrosal is almost identical with that of *Bassariscus*. The internal auditory meatus shows the dorsal foramen for the facial nerve and the ventral foramina for the auditory nerve. The appendicular fossa is larger than the internal auditory meatus. It has an overhanging puckered lip which is also characteristic of the same fossa in the dog. The cat, however, has a small appendicular fossa without the puckered overhanging lip. In *Nassua* the appendicular fossa is shallower than in either *Edaphocyon* or *Bassariscus*.

In summary, the petrosal of *Edaphocyon* on the ventral side has the general shape of that of *Bassariscus* but resembles that of *Nassua* in not having a lip over the foramen ovale. On the dorsal side, the petrosal is more nearly like that of *Bassariscus*. There is no appendicular fossa in *Procyon lotor* so that the dorsal surface of the petrosal in this form is quite different than that in *Edaphocyon*, *Nassua*, and *Bassariscus*. The phylogenetic significance of the appendicular fossa is uncertain. It is large and well developed in *Canis*, *Ursus*, *Urocyon*, and *Bassariscus*, medium size and shallow in *Felis* and *Nassua*, and almost nonexistent in *Procyon*.

Remarks.—Although *Edaphocyon* is procyonid, it is not necessarily in line with any of the living procyonids. Its molar teeth most closely resemble *Bassariscus* since this is the only living procyonid with internal cingula on the molars, but the P^4 is not as sectorial as that of *Bassariscus*. The sum total of its characters preserved would place it in a central primitive position within the procyonids and with certain resemblances to the canids.

TABLE 1—MEASUREMENTS (IN MM.) OF TEETH OF *Edaphocyon pointblankensis*, N. GEN. ET SP.

	Left		Right	
	Length	Width	Length	Width
P2	6.1	2.8	—	—
P4	8.6	7.6	8.7	7.9
M1	7.1	9.3	6.9	9.1
M2	—	7.2 approx.	6.4	7.4

COLD SPRING FAUNA

Subfamily AMPHICYONINAE

AMPHICYON LONGIRAMUS White, 1942

Text-figs. 3a,b; 4a

An M^2 (B.E.G. 31191-22, text-fig. 4a) from the Cold Spring fauna is unworn and beautifully preserved. The paracone is massive and much larger than the metacone. From the internal mid-section of the base of each, a protoconular ridge and a metaconular ridge converge internally into a high cone-shaped protocone. Internal to the protocone is a very broad crenulate cingular shelf. The tooth is about the same size as the M^2 in *Amphicyon riggsi* McGrew (1939, p. 343), but the paracone of the Texas specimen is larger and the protocone much more prominent.

Fragments of a lower jaw of *A. longiramus* (B.E.G. 40418-8, text-fig. 3a,b) were discovered during the process of constructing an underpass just west of Brenham, Washintgon County, Texas. Unbroken P_3–M_2 and the roots of these teeth were preserved in one of the fragments. Since there were no fragments to fill gaps between the tooth-bearing portion of the jaw, the ascending ramus, and the lower angle, the length and depth of the jaw are uncertain.

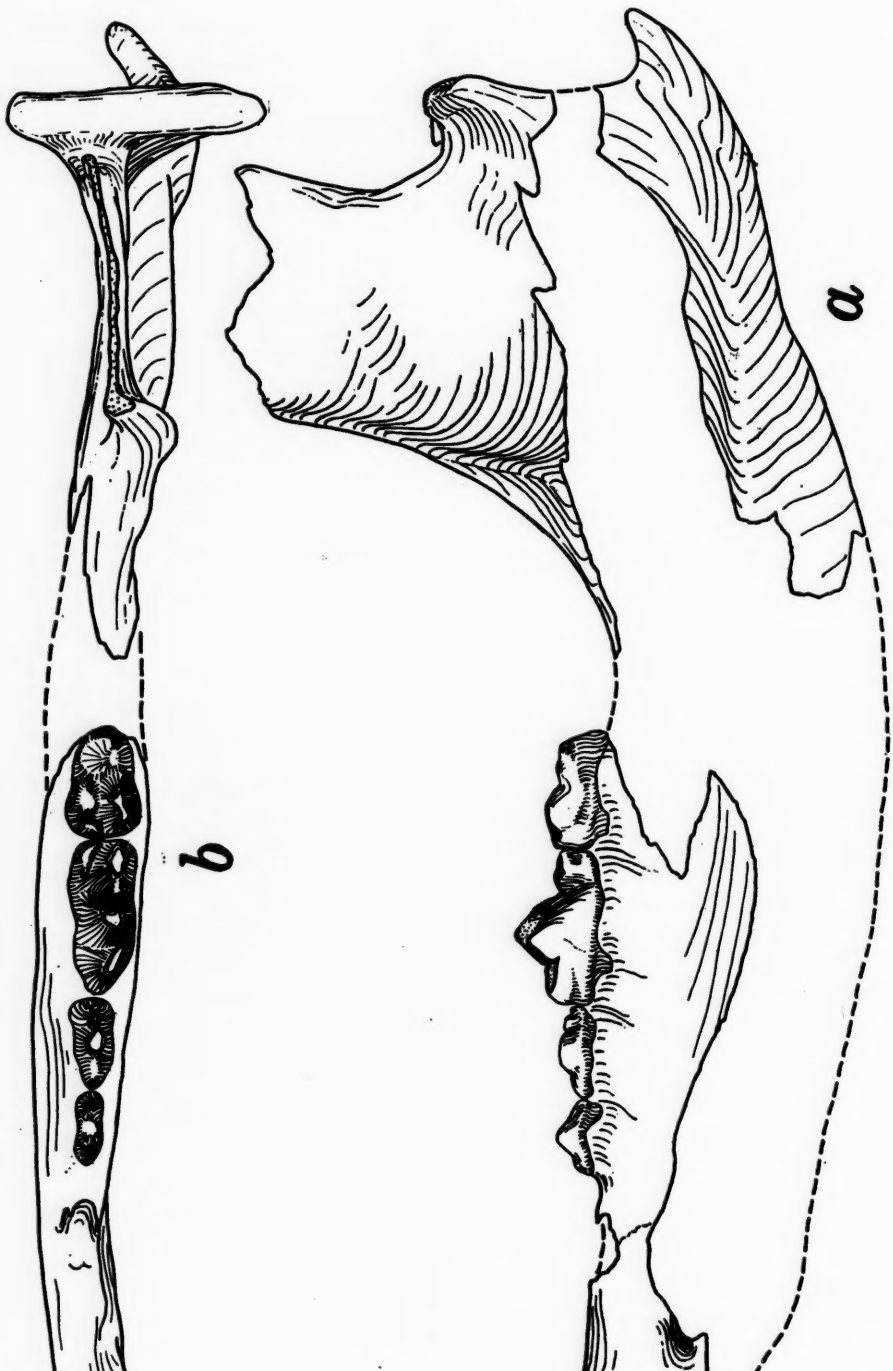
Complete molar teeth of *Protohippus* cf. *vetus* Quinn were recovered from the same road cut. These teeth are slightly longer crowned than *P. vetus* from the Burkeville fauna. This fact plus the occurrence of *Calippus francisi* (Hay) at nearby localities at the same stratigraphic level indicate that the Brenham road cut locality contains a Cold Spring fauna. This extends the range of *Amphicyon longiramus* from Arikareean to Hemingfordian.

The dental series is moderately worn. P_3 is unworn and shows no posterior accessory cusp. P_4 is worn and shows a well-developed posterior cusp as described by Olsen (1958). M_1 is like that of the Florida specimens but on M_2 the protoconid is larger than the metaconid.

AMPHICYON PONTONI Simpson 1930

Text-fig. 2j,k

An M_2 (B.E.G. 40269-1) from near Cold Spring, San Jacinto County, Texas, is so



TEXT-FIG. 3

a,b—*Amphicyon longiramus* White. External and dorsal views of lower jaw fragment. B.E.G. 40418-8. Cold Spring fauna, near Brenham, Washington County, Texas, ×0.6.

small that it seems improbable that it belongs to *A. longiramus*. It is much closer in size to *A. pontoni* Simpson and is tentatively identified as such.

Subfamily BOROPHAGINAE
AELURODON FRANCISI Hay, 1924
Text-fig. 4b–k

This species was described by Hay (1924) from a fragment of a right dentary containing. P_3–M_3. The specimen now bears the number 2379 in the collection of the Texas A. & M. College Museum. Vander Hoof and Gregory (1940) doubtfully refer the species to *Aelurodon* and remark as follows (p. 154):

"In conclusion, *A francisi* may be considered as related to *Aelurodon* rather closely, more particularly to *A. taxoides*. It does not present characters sufficient for positive generic identification, and might belong to either *Cynodesmus*, *Tomarctus*, or *Aelurodon;* the size characters favor inclusion in one of the two genera first named."

The type specimen was recovered from a 22-foot well on the J. Niscavit farm, 3 miles north of Stoneham, Grimes County, Texas. Its stratigraphic position is uncertain, but by projecting the strike of the Fleming formation it most likely occurs in the middle portion and would therefore belong to the Cold Spring fauna.

Aelurodon simulans Hay (T.A.M. 2186) was synonymised with *A. francisi* by Vander Hoof and Gregory (1940). The writer fully concurs with this change. Additional material referrable to *A. francisi* was recovered from the Cold Spring fauna in San Jacinto and Polk counties, Texas, by units of a Work Projects Administration Paleontological Survey Project sponsored by the Bureau of Economic Geology.

Three different types of canids are present in the Texas Miocene faunas: (1) the large *Amphycyon*, (2) small, slender lower-jawed forms belonging to *Cynodesmus* and *Tomarctus*, and (3) a medium-sized, massive lower-jawed type. Since the lower jaws of *Aelurodon* tend to be deeper and more massive than those of either *Tomarctus* or *Cynodesmus* and since the type of *A. francisi* is of this massive variety, specimens exhibiting this character are placed in that species.

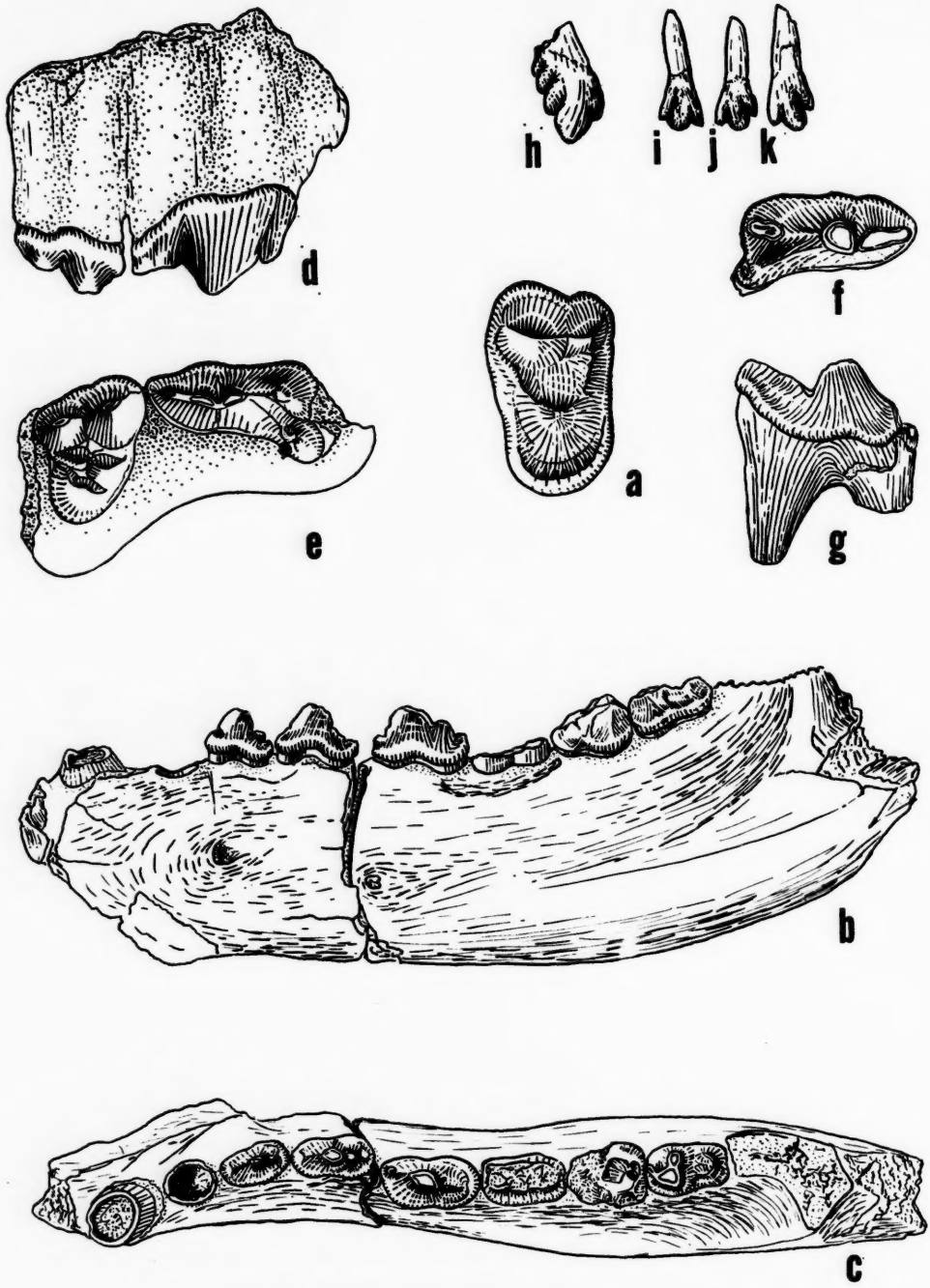
A specimen numbered T.A.M. 2634B (text-fig. 4b,c, posterior portion) agrees very closely in size with *A. francisi*. Each tooth on the Cold Spring specimen is 2 mm. longer than the same tooth on the type. Since the range of variation is unknown and since the stratigraphic level of the type is uncertain, this is felt to be close agreement.

Another specimen (B.E.G. 31191-9, text-fig. 4b,c, anterior portion) from Cold Spring makes a perfect fit with T.A.M. 2634B. Both C. J. Hesse, from Texas A. & M. College, and parties from the W.P.A. Paleontological Survey Project at Austin visited the same locality, and it is evident that these two specimens are parts of the same jaw. On T.A.M. 2634B, P_4 is present, only the heel of M_1 is preserved, M_2 is present, and M_3 is missing.

An almost complete sequence of upper teeth can be made from three specimens: B.E.G. 31191-23 contains P^4, M^1 (text-fig. 4d,e); B.E.G. 31191-30 (text-fig. 4f,g) is a P^4; B.E.G. 31183-72 (text-fig. 4h–k) includes I^1, I^2, and I^3. Also preserved but not figured are M^1 and M^2. The incisors are exactly like those shown by Barbour and Cook (1917, fig. 4) for *A. platyhinus*, referred by Vander Hoof and Gregory (1940) to *A. taxoides*. The canine is crushed and has lost the root; it may be deciduous. The premolar is characteristically stepped posteriorly. Nothing can be told of the spacing because B.E.G. 31183-72 consists of loose teeth.

The carnassial is represented by two specimens. The protocone on B.E.G. 31191-23 (text-fig. 4e) has two distinct cusps while that on B.E.G. 31191-30 (text-fig. 4f) is single. The protocone is pointed anteromedially at about one o'clock with respect to the median line of the tooth. The parastyle is very prominent and arises from a distinct ridge that runs from the anterior edge of the paracone to the protocone. No other unusual features are seen on the paracones or protocone.

M^1 is represented in two specimens. The hypocone on B.E.G. 31191-23 (text-fig. 4e) has two distinct cusps, whereas on B.E.G. 31183-72 (tooth not figured) it is a single ridge. B.E.G. 31191-23 is more worn than B.E.G. 31183-72. The removal of the anterointernal cingulum by wear gives the former the appearance of being more strongly curved posteriorly. The metaconule is more distinct on B.E.G. 31183-72.



TEXT-FIG. 4—All specimens from Cold Spring fauna
All figures ×1

a—*Amphicyon longiramus* White. M^2, B.E.G. 31191-22. Near Cold Spring, San Jacinto County, Texas.

b–k—*Aelurodon francisi* Hay, *b,c*, Anterior portion of jaw, B.E.G. 31191–9; posterior portion of jaw, T.A.M. 2634B, external and dorsal views. Near Cold Spring, San Jacinto County, Texas. *d,e*, P^4 and M^1, external and ventral views, B.E.G. 31191-23. Near Cold Spring, San Jacinto County, Texas. *f,g*, Dorsal and external views, B.E.G. 31191-30. Near Cold Spring, San Jacinto County, Texas. *h–k*, Right I *1,3* and left I *1,2*, outer surface. B.E.G. 31183–72. Near Livingston, Polk County, Texas.

TABLE 2—TABLE OF MEASUREMENTS (IN MM.) OF *Aleurodon francisi* HAY AND *Tomarctus canavus* (SIMPSON)

	T.A.M. 2379: type of *A. francisi*		B.E.G. 31191-9		T.A.M. 2634B (Cold Spring fauna)		T.A.M. 2186: type of *A. simulans*		B.E.G. 31190-67: *T. canavus*	
	Length	Width	Length	Width	Length	Width	Length	Width	Length	Width
P_2	—	—	10	6.1	—	—	—	—	—	—
P_3	9	6	12	7.1	—	—	11	5.5	—	—
P_4	12.8	7.2	—	—	14.1	8.1	13.4	7	—	—
M_1	24	10.5	—	—	24	—	21	—	—	—
M_2	10.5	7	—	—	11.1	8	11.8	7	—	—
M_3	6.5	4.6	—	—	—	—	—	—	—	—
Depth below M_1	—	27.5	—	—	—	32.5	—	27.1	—	19.4

LAPARA CREEK FAUNA

Subfamily AMPHICYONINAE

Text-fig. 5a,b

Amphicyonid upper molars are known from the Lapara Creek fauna. B.E.G. 31132-29 (not figured) is triangular and not posteriorly curved, and 31132-259 (not figured) also is not posteriorly curved but is more quadrangular. Both of these specimens are from beds low in the Lapara member of the Goliad formation. B.E.G. 31184-2 (text-fig. 5a) is from the upper beds and is much larger. This tooth is larger than *Pliocyon walkerae*, Johnston and Christian (1941, p. 59), but is the same size as the M^1 of *Amphicyon frendens*.

A lower M_2 (B.E.G. 31132-328, text-fig. 5b) from the Lapara Creek fauna is amphicyonid. The heel is crested with a massive hypoconid.

A single canine (B.E.G. 31081-1243, not figured) is questionably pliocyonid because of its large size. It bears prominent posterior and antero-internal ridges.

Subfamily BOROPHAGINAE

AELURODON TAXOIDES Hatcher, 1894

Text-fig. 5c,d

A well-preserved left ramus of the lower jaw of *Aelurodon taxoides* (B.E.G. 31132-458, text-fig. 5c,d) is complete except for P_1, M_3, and the posterior margin of the coronoid process. The teeth are worn but the diagnostic characters are distinct.

The size of the Texas specimen agrees closely with *Aelurodon taxoides* and *Tephrocyon mortifer* Cook (1914), which was later synonymised by Vander Hoof and Gregory (1940) with *Aelurodon haydeni*. Although the mandible has been repaired with plaster so that the length of the premolar series is uncertain, it appears that the premolar series is longer than the length of the molar series. This would seem to imply closer relationship with *A. taxoides* than with *A. wheelerianus*, as pointed out by Thorpe (1922).

TABLE 3—MEASUREMENTS OF *Aelurodon taxoides*, B.E.G. 33132-458

	Length (in mm.)
Premolar series	57.3
Molar series	50.0
M_2	12.2
M_1	31.4
P_4	17.8
P_3	13.3
P_2	11.9

Subfamily CANINAE

LEPTOCYON VAFER (Leidy), 1858

Text-fig. 5e,f

A right ramus of the lower jaw (B.E.G. 30896-241, text-fig. 5e,f) is preserved with complete P_2–M_2. Alveoli for P_1 and M_3 are present. P_2 and P_3 are without accessory cusps. P_4 has a small accessory cusp about halfway up the posterior edge of the main cusp. There is no basal cusp either anteriorly or posteriorly. The premolars are closely spaced but not crowded. The heel of M_1 is trough-shaped with the hypoconid much larger than the entoconid but with the two of them sufficiently large to leave the posterior margin of the tooth open. M_2 has no

visible paraconid. The metaconid is slightly larger than the protoconid. The hypoconid is a distinct but low cusp, but the entoconid is only a slight rise on the edge of the tooth. Both P_1 and M_3 were small and single rooted.

Canid indet.
Text-fig. 5g

A badly worn right maxilla (B.E.G. 31081-1255, text-fig. 5g) is the same size as the small coyote which inhabits central Texas and northern Mexico today. From the size and morphology of the teeth, it is impossible to distinguish the fragment from *Canis*, but the specimen is so fragmentary that it is felt necessary to await the discovery of better material before making more definite assignment. It is at this time during the late Miocene or Early Pliocene that *Canis* evolved from *Tomarctus*, and it is also a time when the remains of the smaller unspecialized group of dogs are poorly represented by fossil material. It is for the latter reason that this specimen is mentioned. The smaller dogs were present in this area, living with *Amphicyon* and *Aelurodon*.

Discussion of Amphicyon.—The genus *Amphicyon* has been reported in the New World from Nebraska, Colorado, Oregon, Montana, California, Florida, and Texas, questionably from Nevada and Honduras. With the exception of Florida and Texas, its time range seems to be late Hemingfordian to Clarendonian. In both Florida and Texas *Amphicyon* is found with faunas that are interpreted as being late Arikareean. Only in the Garvin Gulley fauna of the Texas Coastal Plain has *Amphicyon* been found associated with the characteristic Arikareean genera *Daphaenodon*, *Dinohyus*, and *Parahippus*. In the Old World, *Amphicyon* has time range from Chattian to Pontian.

Peterson (1910), Matthew (1924), Scott and Jepsen (1936), and McGrew (1939) have thought that *Daphaedon* was ancestral to *Amphicyon*. Hough (1948b), however, working with morphological characters other than the dentition disclaims a direct ancestral relationship between these two genera. She recognizes close relationship but would not propose that it be closer than a subfamily level. She states (Hough, 1948b, p. 574), however, that . . . "until the Arikareean, at which time the daphoenid group had given rise to the gigantic bear dogs." She includes the genus *Amphicyon* in the family Daphoenidae.

It seems strange since *Amphicyon* is properly a European genus, having been originally described by Lartet (1836) and having a range in Europe as far back as the Chattian, that Matthew, Scott and Jepsen, and McGrew should argue for a North American origin of the genus and derive it through the daphoenids.

Matthew's (1924) phylogeny was questioned by Helbing (1928) who points out that M^3 is present in *Amphicyon* and that there is very probably no European group of daphoenids. In the daphoenids the M^3 is strongly reduced or absent. *Daphaenodon superbus*, as figured by Peterson (1910), has an M^3 almost two and a half times smaller than M^2 whereas the M^3 of the Garvin Gulley *Amphicyon* is estimated to be only one and a half times smaller.

Simpson (1947) attributes the earliest known occurrence of *Amphicyon* to the Late

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TEXT-FIG. 5—All specimens from Lapara Creek fauna
All figures ×1

a,b—Amphicyonid. *a*, M^1, B.E.G. 31132-29. *b*, M_2, internal view, B.E.G. 31132-328. Both from near Normanna, Bee County, Texas.
c,d—*Aelurodon taxoides* Hatcher. Dorsal and interal views of lower jaw fragment, B.E.G. 31132-458. Near Normanna, Bee County, Texas.
e,f—*Leptocyon vafer* (Leidy). Dorsal and internal views, B.E.G. 30896-241. Near Berclair, Bee County, Texas.
g—Canid indet. Dorsal view, B.E.G. 31081-1255. Near Berclair, Bee County, Texas.

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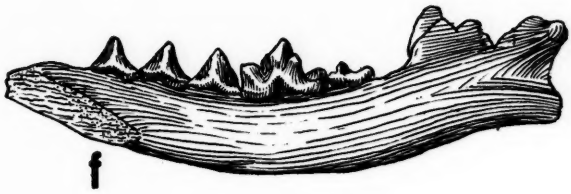

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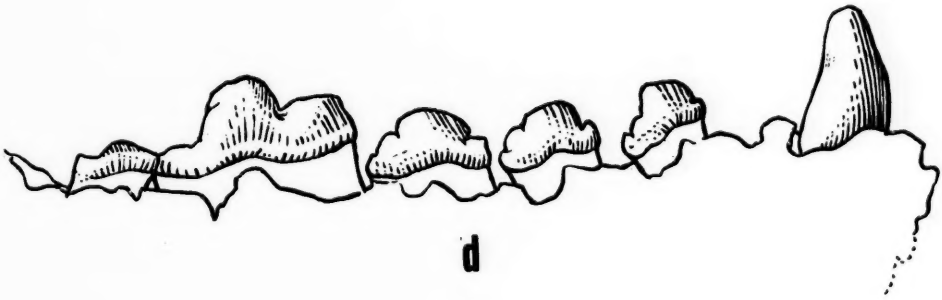

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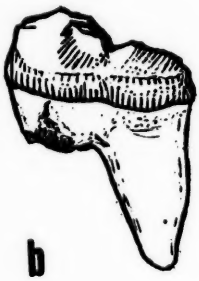

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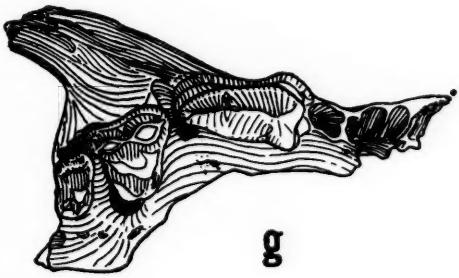


g

Oligocene of Europe. Stirton (1951) states that "True *Amphicyon* is found in the Sheep Creek. Evidently this genus came to America shortly before *Miomastodon*, which has not been found in the large Sheep Creek fauna nor in the Thomas Farm assemblage." A mastodont, listed as *Gomphotherium* by Quinn (1955), is present in the Cold Spring fauna on the Texas Gulf Coast. The Cold Spring fauna is considered to be middle to late Hemingfordian, as set forth by Quinn (1955).

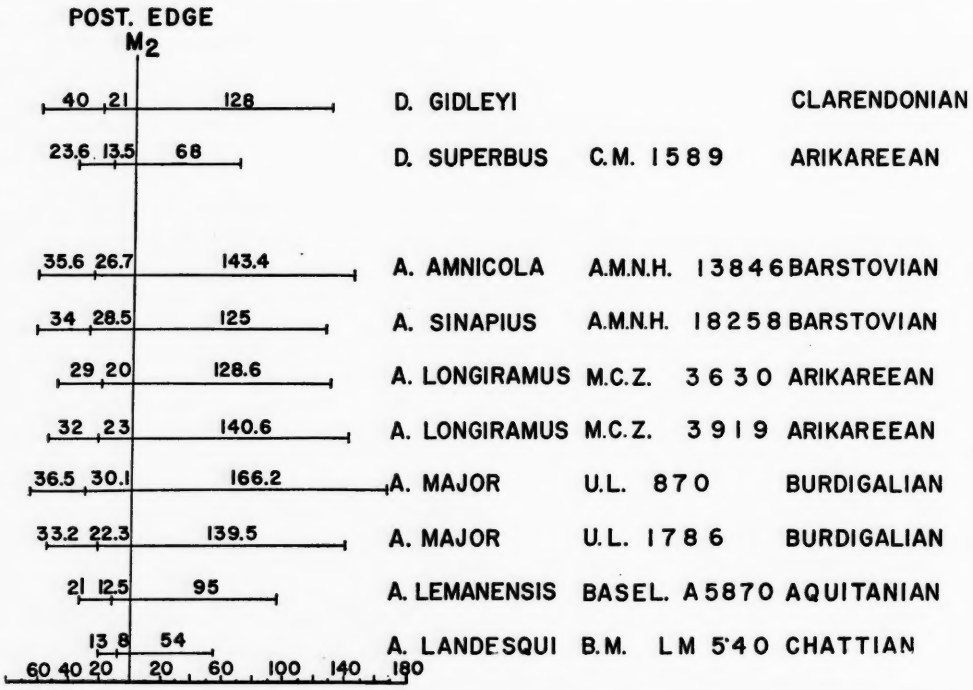
An examination of the amphicyonid material at the Naturhistorische Museum, Basel, Switzerland and in the collections of the Geological Institute of the University of Lyon, France show that *A. longiramus* is very similar to *A. major* in dental characters. *A. longiramus* falls within the size range of specimens in both those museums identified as *A. major*.

The amphicyonines on both sides of the Atlantic show other characters in common. The dental formula given for *Amphicyon* usually includes three incisors for both upper and lower jaws. In specimens of the muzzle examined by the writer there are three upper incisors. This area is especially well preserved on I.P.H.G. 12296, *A. dietrichi*, a cast of which was kindly supplied by Prof. Richard Dehm. In this specimen, I^1 and I^2 are greatly reduced and I^3 is enlarged.

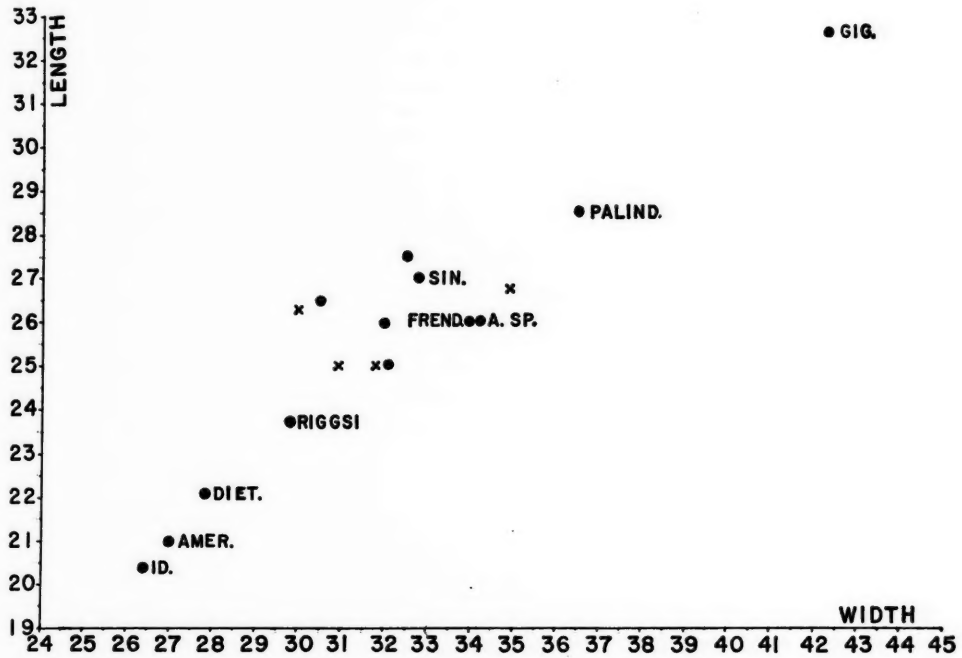
Lower jaws on which the symphyseal region is preserved are not common, but there is evidence that the number of lower incisors was only one or possibly two.

A. lemanensis (B.M. Au917) from Saulcet (near Chavroches), France has alveoli for one or possibly two lower incisors. *Amphicyon* sp. (B.M. Sau. 25) from near Varennes sur Allier of Middle Aquitanian age has the symphyseal suture present. Only a single alveolus is present between the suture and the large alveolus for the canine.

A. frendens (A.M.N.H. 18913), a juvenile, has an alveolus for dC and another for C


POST. EDGE
M2
40 21 128 D. GIDLEYI CLARENDONIAN
23.6 13.5 68 D. SUPERBUS C.M. 1589 ARIKAREEAN
35.6 26.7 143.4 A. AMNICOLA A.M.N.H. 13846 BARSTOVIAN
34 28.5 125 A. SINAPIUS A.M.N.H. 18258 BARSTOVIAN
29 20 128.6 A. LONGIRAMUS M.C.Z. 3630 ARIKAREEAN
32 23 140.6 A. LONGIRAMUS M.C.Z. 3919 ARIKAREEAN
36.5 30.1 166.2 A. MAJOR U.L. 870 BURDIGALIAN
33.2 22.3 139.5 A. MAJOR U.L. 1786 BURDIGALIAN
21 12.5 95 A. LEMANENSIS BASEL. A5870 AQUITANIAN
13 8 54 A. LANDESQUI B.M. LM 540 CHATTIAN
60 40 20 20 60 100 140 180

TEXT-FIG. 6—Measurements in millimeters of lengths of M_1 and M_2 and distance from the posterior edge of M_2 to the condyle of the lower jaw of various species of *Amphicyon* compared with *Daphaenodon superbus* and *Dinocyon gidleyi*. The age of each is also given.



TEXT-FIG. 7—Length-width diagram in millimeters of M^1 of various species of Amphicyon from Europe and North America. ● (without name), *A. longiramus;* × (without name), *A. major;* AMER., *A. americanus;* DIET., *A. dietrichi;* FREND., *A. frendens;* GIG., *A. giganteus;* ID., *A. idoneus;* PALIND., *A. palindicus;* RIGGSI, *A. riggsi;* SIN., *A. sinapius; A.* sp., *A.* sp., Lapara Creek fauna.

just posterior to the first. Medial to these are two alveoli one behind the other. I interpret these as dI and a permanent I. This would mean that only a single lower incisor was present in this form.

A. riggsi (C.N.H.M. P12029) has a small portion of the symphysis present. Although the area is poorly preserved, there seems to be only a single alveolus median to that for the canine.

In contrast, *Daphaenodon superbus* has three well-preserved lower incisors of approximately equal size, a distinctly different arrangement than that found in *Amphicyon.*

The proportions of the skull and lower jaw in *Amphicyon* are different than those found in *Daphaenodon.* In *Amphicyon* the skull is extremely elongate, the elongation having taken place posterior to the molar teeth and anterior to the opening for the Vth nerve. This is reflected in the lower jaw by elongation between M_3 and the condyle (text-fig. 6).

A. major (U.L. 870 and U.L. 1786) and *A. longiramus* (M.C.Z. 3919, M.C.Z. 3630) distinctly show this elongation. A comparison of the length of M_1 and M_2 and the distance from the posterior end of M_2 to the condyle is shown in text-figures 6,7. These specimens and others of different species of *Amphicyon* are compared with *Daphaenodon* and *Dinocyon gidleyi.* M_1 and M_2, while very large teeth individually, occupy proportionally less of the total length of the lower jaw than do the teeth of *Daphaenodon.*

The retention of the proportionally large M3 in the amphicyonines has already been mentioned.

Hough (1948a,b) points out differences in the skull between *Amphicyon* and *Daphaenodon.* In her first paper (Hough, 1948a) she places *Amphicyon* in the family Ursidae but

in her second paper (Hough, 1948b) in the family Daphaenidae. In this later paper she states (p. 600): "It seems probable, therefore, that *Amphicyon* and *Daphaenodon* represent different branches of the same subfamily rather than having a directly ancestral relationship and that neither is in direct line with the bears."

From the evidence presented by Hough (1948a,b) on the auditory region, the reduction of the number of lower incisors, and the different proportions of the lower jaw, it now seems clear that *Amphicyon* is not a direct descendent of *Daphaenodon*. A much more probable interpretation would now be that *Daphaenodon* and *Amphicyon* arose from a common stock in Eurasia during the Eocene. *Daphaenus* then spread to North America and had arrived by Oligocene time, while *Amphicyon* remained in Eurasia. The appearance of *Amphicyon* in the Arikareean is the result of a later migration to North America.

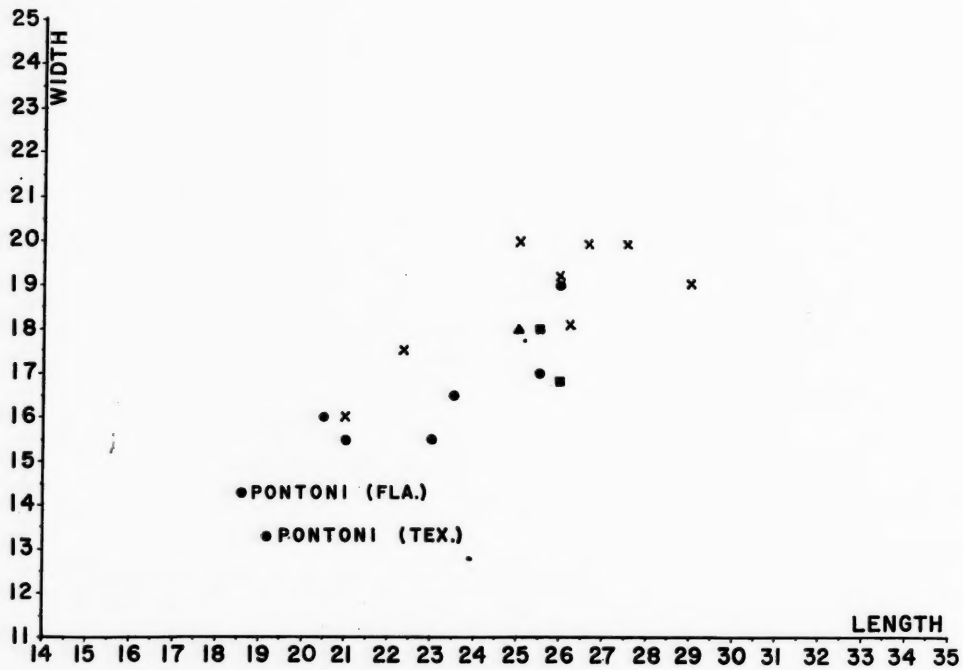
Discussion of Aelurodon.—Quinn (1955) presented preliminary evidence for the Hemingfordian age of the Cold Spring fauna. Vander Hoof and Gregory (1940) consider the range of *Aelurodon* to be Late Miocene and Early Pliocene and agree that the size of *A. francisi* is so small that it may be excluded from the genus. The morphological characters of the Cold Spring form very definitely agree with *Aelurodon*, and by the criteria of Vander Hoof and Gregory it must be included within the genus.

Text-figure 9 shows a length-width plot for M_1 of several species of *Aelurodon* and *Tomarctus canavus*. Table 2 shows comparison of the depths of the lower jaw below M_1. In both the chart and the table, *A. francisi* is closer to the other species of *Aelurodon* than to *Tomarctus*.

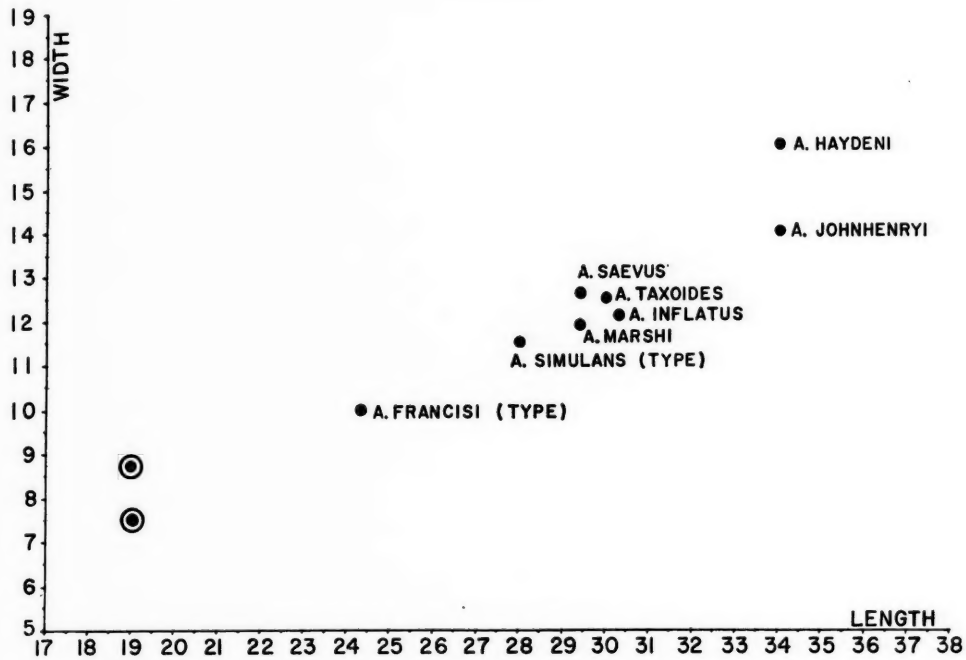
CONCLUSIONS

Daphaenodon is recognized in Texas for the first time, where it is found associated with *Amphicyon*.

Amphicyon, a European genus, spread to



TEXT-FIG. 8—Length-width diagram in millimeters of M_2. dot without name, *Amphicyon longiramus* from Florida. triangle, *A. longiramus* from Texas. ×, *A. major* from various European localities. square, Amphicyonid from the Lapara Creek fauna.



TEXT-FIG. *9*—Length-width diagram of M_1 of various species of *Alurodon* to show intermediate size of the type of *A. francisi* and Texas specimens of *Tomarctus canavus* (circled dots).

North America during late Early Miocene time and is found on the Gulf Coast in rocks of that age to latest Miocene or earliest Pliocene. On the basis of the presently known material, both *A. pontoni* Simpson and *A. longiramus* White can be identified.

Aleurodon francisi Hay is reconfirmed as belonging to that genus. The presence of *Tomarctus canavus* (Simpson) and *Cynodesmus iamonensis* (Sellards is recognized, which extends the range of these species from Florida to the Texas Coastal Plain.

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DEVELOPMENT OF PALEONTOLOGY

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ABSTRACT—Four periods can be recognized in the development of paleontology. The first, or pre-scientific period, began with the ancient Greek philosophers and continued to the mid-eighteenth century. Almost no progress was made during these 2000 years. Fossils, correctly interpreted by some of the ancients, came to be recognized as organic objects. Various ideas were expressed regarding both rocks and fossils but very few observations of any real scientific value were made.

The second, or early scientific period, lasted for about 100 years and ended in the mid-nineteenth century. During this time, geologic understanding rapidly advanced and fossils attracted increasingly wide attention because of their strange nature and usefulness in correlation. Evolutionary theories originated but religious beliefs caused their general rejection.

The middle scientific period began with Darwin and continued for most of the remaining nineteenth century. Evolution as a process gained wide acceptance and was applied in paleontology but its mechanism was unsatisfactorily explained.

The modern scientific period has been marked by the perfection of genetic theory and its application to paleontologic studies. Biologic interest in fossils slowly but steadily expanded. Increasing consideration was given to the recognition of evolutionary patterns and proof of evolutionary theory. Geologic interests in fossils shifted gradually from their practical applications in correlation to paleoecology and its promise of providing a better understanding of physical environments of the past.

INTRODUCTION

MODERN science is the product of many active minds that have been concerned with facts and theories. Progress has been uneven and periods of rapid advancement have been separated by others of relative stagnation or even retrogression. Each advance has been stimulated by a basic idea or combination of ideas that opened up new pathways to speculation and the development of hypotheses. These have been tested by observation and the accumulation of new evidence. Inevitably, many hypotheses were incorrect and have been rejected, and these are no longer of much scientific interest. They may have been important historically, however, because they either inhibited or stimulated thinking, and opposition to them may have sparked the emergence of new and sounder views.

Ideas at first generally are very tenuous and evanescent things. They may originate in wild imaginings, as flashes of inspiration, or result from long and careful thought. They may start as a mere germ, to be followed by slow perfection, or they may burst forth in beautiful completeness. The same idea can occur independently to different persons, and certainly some have. Many, however, owe their development to a process of mental fertilization, and an individual may not realize his debt to inspiration derived from others. In a world where minds communicate, no idea arises in a vacuum, and the source of many ideas is obscure. Generally, the actual details of their origin and unfolding cannot now be known completely.

The ideas, conclusions, and theories that mark the development and gradual advancement of paleontologic science range widely through certain aspects of both geology and biology. The space of a few pages, obviously, is inadequate for a thorough consideration of these matters but the main outlines can be presented. For this purpose, a group of outstanding persons has been chosen by whose lives and works the development of paleontology can be traced, although numerous others, perhaps, were of equal or only slightly less importance.

PRE-SCIENTIFIC PERIOD

Aristotle and Greek Natural Philosophy.—Consideration of most sciences customarily begins with a review of the thoughts and opinions of the ancient Greek philosophers, extending back six centuries or more before

the opening of the Christian era. Most of the writings of this time are known only in fragmentary form, and all of the conclusions drawn from them do not seem sound. Modern commentators are too inclined to read meanings into ancient words that stem from their own beliefs or particular trains of thought.

No opinions concerning the organic world before Aristotle's time are especially significant. Vaguely, a trend can be discerned beginning in classical mythology and gradually making contact with reality through observation and reason. The belief was widely held that living things arose spontaneously from water, the earth, or other substances. This idea was not finally abandoned until Pasteur performed his experiments with fermentation in the latter half of the nineteenth century.

Some historians are inclined to trace the idea of evolution to Anaximander (611–547 BC) because he suggested that men have been derived from fish. Xenophanes (576–480 BC) recognized that fossils are the remains of once living animals, and he concluded that the sea formerly submerged the earth. Empedocles (495–435 BC) believed that plants, animals, and man appeared in this order because each is dependent upon its predecessors for survival. He saw no purpose or plan in this succession, however, and supposed that life, by chance, assumed innumerable experimental forms. Among these were centaurs, chimeras, and other creatures of hybrid form which became extinct because they were not suited for survival. Anaxagoras (500–428 BC) attributed the adaptation of animals to their varied ways of life to an intelligent guiding principle inherent in nature from the most remote beginning.

Aristotle (384–322 BC) was one of the most remarkable men in all recorded history whose influence was paramount in scientific thought down to the beginning of the modern epoch and, in a lesser degree, even to the present time. He was born in Macedonia, son of the court physician, and early in life acquired a broad interest in nature. He studied in Athens under Plato, travelled for several years, and became the tutor of Alexander the Great until this young man succeeded to his father's throne. Subsequently, he returned to Athens where he established his own school. Aristotle's writings covered a wide range of intellectual subjects, known under a total of 140 titles, but only about 40 have survived to the present day.

Aristotle recognized a single chain in nature with gradual transitions from inorganic objects to plants and animals that culminates in man. Members of this sequence were not necessarily descended from each other. Progression was accomplished by the action of an inner guiding purpose that pervades all things and strives continually for more and more perfection. Chance played no part in this process nor was it achieved simply by the survival of the fittest. Aristotle was not an evolutionist in any modern sense.

Thus, Greek thought presented two contrasting views: (1) that nature is mechanistic and operates by the laws of chance with no evidence of purpose (Empedocles), and (2) that nature follows definite paths either ordained in the beginning (Anaxagorus) or guided by intelligent design (Aristotle).

Avicenna and Islamic Natural Philosophy.—After the breaking up of Alexander's empire, the intellectual life of Greece degenerated and lost much of its spontaneity. As the western world gradually sank into the lethargy of the Middle Ages and Christianity spread westward, the influence of ancient Greece declined and Greek thought was soon forgotten. At the same time, the rise of Mohammedanism among the Arabs resulted in the rapid spreading of an aggressive culture eastward into India and westward across north Africa into Spain. With it there developed a new interest in philosophy and science. Aristotle's works were translated into Arabic in the ninth century, and for several hundred years these strongly influenced Islamic thinking.

Avicenna (979–1037), or more properly Abu Ali al-Husain ibn Abdullah ibn Sina, was a Persian physician and the greatest of Islamic philosophers. He combined Aristotelianism with oriental mysticism, believing in a creation but also in an orderly shaping of the earth by natural processes.

Eastern manuscripts reached Spain in the tenth century and Cordova became the intellectual capital of that country. Several of the writers there enthusiastically ac-

cepted Aristotle's views with certain modifications. Abu'l-Walid Mohammed ibn Ahmid ibn Mohammed ibn Roshed, or Averroes (1126–1198) a judge and physician, however, denied creation and immortality of the soul. In the twelfth century, Arabic literature began to be translated into Latin, and eastern writings, including Aristotle's works, first came to the notice of western scholars. In 1209, the Provincial Council of the Church in Paris ruled that this literature was heretical and, under an interdict, forbade its study.

This period was not important for scientific progress or the development of new ideas. It preserved and passed on, however, some of the culture of the ancient world that might otherwise have been lost. This greatly influenced subsequent western European thought.

Bacon and Scientific Observation.—Hypotheses may be reached in two different ways both of which conform to what has been called the look and guess method. The first requires relatively little knowledge and consists mainly of reasoning backward from a conclusion in an attempt to build up a logical framework of support. This is deductive reasoning and it is characteristic of most philosophical thinking which ordinarily does not seek for factual proof. Greek opinions regarding nature were arrived at largely in this way.

Roger Bacon (1220–1292), one of the most brilliant men of the late medieval period, was descended from a wealthy English family and became a Franciscan monk. He wrote extensively on many subjects. Although he contributed little to the actual advancement of knowledge, Bacon's approach to science was essentially modern and, in this respect, his thinking was far in advance of his times. He was highly credulous in some respects but vigorously advocated experimentation and extensive observation as the only reliable means of arriving at valid conclusions. This is the inductive method of reasoning that builds a theory upward from a body of accumulated evidence. His ideas were further developed more than 300 years later by the more famous Francis Bacon (1561–1626).

Aristotle was aware of the advantages of induction but the knowledge available to him was not adequate for a very successful approach to natural science in such a way. Gradually, the situation changed but inductive reasoning, as applied to matters of paleontologic interest, did not reach full development until the time of Hutton in geology and Charles Darwin in biology.

Gesner and Fossils.—The Middle Ages in Europe was a long period of general intellectual stagnation and it witnessed practically no scientific progress. The organic nature of fossils had been recognized by several of the early Greeks but many later writers, who had no conception of anything but a static earth, sought to explain their occurrence in various fantastic ways. Bones of large size were attributed to dragons or other mythical monsters, or to antediluvian human giants. Shells resembling organisms of the sea were interpreted to be the results of unsuccessful attempts by nature to produce life, fermentations within the rocks, growths produced under the influence of comets or other heavenly bodies, the products of germs or seeds carried by ocean mists, or objects created for the express purpose of confusing credulous humans. A few more reasonable and clear sighted persons, however, recognized that fossils are the remains of once living organisms, but it was not until the eighteenth century that this view began to prevail among educated men.

Before fossils were better understood, they commonly were classed with other objects such as minerals, concretions, curiously shaped rocks and Stone Age implements, and the word *fossil* originally included all such things. As curiosities, these attracted considerable attention. The first book describing them was published in 1565 by a Swiss scholar, Conrad Gesner (1516–1565). It was illustrated with very crude wood-cuts but the general nature of several of the fossils is clearly recognizable. A more interesting and much better illustrated book was published by a Welch antiquarian, Edward Lhuyd, in 1699. His was one of the last books that failed to accept the organic nature of fossils.[1]

The seventeenth and eighteenth centuries saw a considerable advance in geologic understanding. The organic nature of fossils

[1] Dr. E. C. Stumm reports that the first North American fossil was illustrated by Martin Lister in 1685. It was a specimen of *Ecphora quadricostata* from the Miocene of Maryland.

generally was admitted but they were commonly explained as relics of Noah's flood. A school of religious geologists grew up, particularly in England, who fitted their explanations to the biblical account of Genesis. Their views prevailed for more than 200 years and were not overcome until after Charles Darwin's time. Paleontologic literature improved, however, from its very low scientific level, and increasingly elaborate and well illustrated books were published indicating interest in this subject by wealthy and well educated persons.

Suarez and Genesis.—Aristotle's views, which were easily accommodated to a theistic pattern, were revered by the early Christian philosophers. St. Augustine (354–430) held that knowledge derived from careful observation and sound reasoning is not necessarily contradicted by the scriptures which can be interpreted figuratively. Thomas Aquinas (1225–1274) concurred in this opinion.

The conflict between science and religion, that has disturbed the thinking of many persons up to modern times, did not become serious until the end of the sixteenth century. Few people previously had the knowledge, interest, or leisure to pursue science, and questions of this kind rarely arose among the small educated class. A man who played an important part in this matter was Francisco Suarez (1548–1617), a Jesuit priest and Spanish theologian of high authority, who may be regarded as the original fundamentalist. He insisted most vigorously on the literal accuracy of the biblical account of Genesis. This rapidly became the orthodox view which, unfortunately, is still held by many relatively uninformed people.

Ray and Species.—Implicit faith in the biblical story was shared by almost all Europeans. This carried with it belief in the special creation of every species of plant and animal. As observations accumulated, however, and as natural science collections grew, more and more variation was noted and increasingly great difficulty was experienced in defining and distinguishing between species of similar kinds. This difficulty was felt particularly in botany which, as a study, advanced more rapidly than zoology. In fact, the view became common among naturalists that species are more or less arbitrary things. For example, some believed that a seed produced by one species might unpredictably germinate and grow into a species of another kind.

John Ray (1627–1705), also spelled Wray, has been considered the Father of English Naturalists. He was the son of a blacksmith but obtained a classical education at Cambridge. He was a fellow of the university until 1649 when he was forced to leave because of his unconventional ideas. Ray was primarily a botanist but, like most other early naturalists, was interested in many other subjects including geology. He is principally remembered for a classification of plants based on their flowers and fruits that influenced Linnaeus' later classification. Ray recognized species by permanence of form, believing them to be immutable, and contended that morphological similarity of parents and offspring is a universal rule. He was the first to emphasize infertility with others as a test of species.

Linnaeus and Binary Nomenclature.—The great voyages of discovery by Portuguese and Spanish navigators in the late fifteenth and early sixteenth centuries were followed by an unparalleled era of exploration and colonization which took Europeans to many distant and strange lands. Reports of their adventures and observations produced an extensive literature that included accounts of many curious plants and animals. Specimens were brought back to Europe in increasing numbers and variety, and they greatly stimulated interest in all branches of natural science.

The efforts of naturalists to describe and classify the novel forms of life with which they thus became acquainted was impeded by ignorance and lack of system. Many of their works were written in Latin, and the animals and plants were given Latin names. These generally were descriptive, and many of them were cumbersome expressions consisting of several words. Practice varied greatly and, as names multiplied, confusion added to the difficulties of understanding.

Carl von Linné (1707–1778), better known by his Latinized name Linnaeus, was the son of a Swedish clergyman. As a boy, he developed an intense interest in botany, but was an indifferent scholar and made unsatisfactory progress in the kind of classical

education offered at that time in Sweden. He was attracted to medicine, however, and after studying in Holland, visited France and England, and returned to Sweden where he practiced as a physician. Later, he became successively professor of medicine and of botany at the University of Uppsala.

Linnaeus is known principally for his systematic lists of plants and animals which were the first extensive works consistently to employ binary nomenclature, or the combination of generic and specific names. His *Species Plantarum* of 1753 and the fifth edition of his *Genera Plantarum* of 1754 are accepted as the starting point of modern botanical nomenclature. Similarly, the tenth edition of his *Systema Naturae* of 1758 is the base of zoological nomenclature. By agreement among biologists, priority in the scientific names of organisms is not recognized for any older literature.

Linnaeus' influence was very great because his classification, based on morphologic similarity, provided naturalists with the means of identifying and naming organisms in a systematic way. He was primarily a cataloger, however, and did little to advance scientific concepts or add to the more fundamental knowledge of biology. His classification gained wide approval and united most biologists in the conclusion, previously expressed by Ray, that all species are morphologically consistent units.

EARLY SCIENTIFIC PERIOD

Buffon and Evolution.—George Louis Leclerc, Compt de Buffon (1707–1788), was the first great natural scientist to appear at the beginning of the modern era. He was the son of a French lawyer and civil servant and, as a boy, developed an abiding interest in science. His earliest investigations involved physical experiments. At the age of 25, he inherited a large fortune from his mother and thereafter devoted himself exclusively to the study of nature. In 1739, he was appointed keeper of the royal gardens and museum whose collections directed his attention more particularly to zoology. In 1849, he began the publication of an exquisitely illustrated series of quarto volumes, that finally reached a total of 44, in which he presented accounts of all the animals known to him. This was the first important organized work on natural science.

Buffon's work has been belittled by some reviewers partly because he was judged to have indulged in unjustified generalizations but, more particularly perhaps, because his unorthodox views ran counter to common prejudices. Buffon was reported to have been exceedingly vain with regard to his personal appearance and literary skill, but he had exceptionally wide interests, great originality, and unflagging industry. He rejected all conclusions concerning science not based on observations. Although he may have believed in the biblical account of a creation and the flood, in his later years at least, he refused to allow these supposed historical events to interfere with the actual evidence as he saw it.

In order to understand the organic world, Buffon believed it necessary first to understand the earth. His geologic conclusions were unusual for his time and some of his ideas anticipated the theories of later scientists who have been held in more esteem. He recognized that fossils prove much of the land to have been submerged beneath the sea. He realized that their occurrence in many kinds and great thicknesses of sediments and rocks could not be explained by Noah's flood but that they date back to more ancient and long continued time. Also, he observed that some fossils represent species now extinct. Buffon noted and understood erosion of the land and the transportation and deposition, in layers, of the sediment so produced. His explanation for changes in the distribution of land and sea did not demand the intervention of catastrophies or supernatural happenings to the same extent as the theories of other eighteenth century writers.

Buffon may be best remembered for his views on evolution. He classed the 200 or more species of mammals, with which he was acquainted, into a small number of families (termed by him genera) on the basis of their form, structure, and behavior. Although his statements are somewhat confused and in part contradictory, he evidently believed that animals, produced at the creation, migrated extensively, and because of differences in climate and food, varied and diverged until a family consisting of several species had been formed. Be-

cause he believed that most variation resulted in smaller individuals, he referred to changing form as "degeneration" rather than as evolution. Buffon had much more than a vague understanding of ecology and remarked upon the climatic control of faunal composition. Finally, similarities in the faunas of the Old and New Worlds led him to conclude that extensive intercontinental migrations had occurred, followed by variation that produced new species.

Lehmann and Stratigraphy.—Fossils and minerals were observed and wondered about long before such common things as rocks aroused much interest. Speculations regarding the origin of mountains finally directed attention to the rocks of which the mountains are composed, and in the eighteenth century, a classification first applied to mountains was transferred to rocks. This resulted in a three-fold division and the beginning of a better understanding of geologic time. The oldest or primitive rocks, dating from the creation of a chaotic world, are crystalline and contain no fossils; secondary rocks are layered, fossiliferous, and date from Noah's flood; and tertiary rocks are unconsolidated and of more recent origin. The principle of superposition was understood and the relative time values of strata in a vertical sequence gradually came to be appreciated.

Johann Gottlob Lehmann (1719–1767), professor of mineralogy at Berlin and St. Petersburg, recognized such a succession of rocks in Germany. He was one of the first geologists to measure and record actual sections of stratified rocks. He studied the Permain beds of northern Germany and distinguished divisions some of which are still recognized. Similar work was conducted by Georg Christian Füchsel (1722–1776) in central Germany where Triassic strata are well developed. Füchsel originated the idea of geologic formations which consist of rocks of similar composition and origin. These concepts were adopted and further developed by Abraham Gottlob Werner (1750–1817), professor of mineralogy at the School of Mines of Freiberg in Saxony. He was the most influential teacher of his time and attracted students from all parts of western Europe.

Although many of Lehmann's and Werner's conclusions were unsound, their work initiated a new era in geologic investigations. Rocks were more carefully observed and they were roughly correlated. Certain generalizations were made and notice began to be taken of possible past changes in geography, climate, and the organisms preserved as fossils.

Hutton and Uniformitarianism.—The effects of running water with respect to the erosion, transportation, and deposition of sediment and the burial of fossils had been noticed and at least partly understood by various persons including Herodotus (484–424) in Egypt, Avicenna in Persia, and Leonardo da Vinci (1452–1519) in Italy, as well as some later writers. James Hutton (1726–1797), however, was the first to appreciate fully the part that these processes have played in the history of the earth. He became convinced that all rocks consist of material produced by the wasting away of other rocks. This necessitated the conclusion that the earth is very old. His reference to a "succession of worlds, with no vestige of a beginning—no prospect of an end" was out of harmony with the generally held opinion that the creation had occurred in the year 4004 BC.

Hutton, the son of a Scotch merchant, successively studied law, medicine, chemistry, and agriculture, and is famous as the first modern geologist. He formulated the principle known as uniformitarianism which holds that all rocks and other features of the earth can be explained on the basis of processes now in operation, and that they do not require the intervention of strange conditions or catastrophies such as had been postulated by most previous geologists. Hutton's views were vigorously opposed but the advocacy of influential friends and followers, among them John Playfair and Sir Charles Lyell, and the accumulation of evidence gathered in many lands slowly gained for them widening recognition.

Uniformitarianism is one of the most important principles of geology and it revolutionized thinking in this field of science. Half a century later, it found almost equal application in biology.

Smith and Stratigraphic Paleontology.—Fossils had been observed and correctly identified as the remains of once living

organisms from very ancient times. Over the course of years, however, two great battles had to be fought and won before paleontology achieved for itself a rational status. The first established the understanding that fossils are organic rather than inorganic "sports of nature." The second banished the idea that they are relics of Noah's flood.

Robert Hooke (1635–1703), the brilliant English mathematician and physicist, seems to have been the first to point out clearly that fossils provide historical evidence of past conditions on the earth. He likened them to ancient coins and manuscripts. Also, he considered the possibility that some represent extinct species but others may be found still living somewhere in the world today. The latter idea persisted into the nineteenth century, and one of the purposes of the Lewis and Clark Expedition after the purchase of Louisiana was to search for living descendants of the Pleistocene mastodons found fossil in the eastern states.

Jean Etienne Guettard (1715–1786), a French botanist and keeper of the natural science collection of the Duke of Orleans, appears to have originated the idea that different fossils might identify different stratigraphic zones. He attempted to make correlations on this basis between regions as far apart as Europe and eastern North America but without particular success.

Stratigraphic paleontology generally is considered to have had its origin in the observations of William Smith (1769–1839), an English surveyor and engineer whose work in coal mines, canal construction and swamp drainage directed his attention to the rocks and their contained fossils. He noted particularly the stratigraphic and faunal successions of the Jurassic System and demonstrated that predictions can be made regarding the occurrence of certain fossils in certain layers and, conversely, that the order of layers can be determined by their fossils. Smith's discovery provided the key that greatly accelerated stratigraphic geology in England and he has been termed Father of English Geology and Father of Stratigraphy.

At about this same time the paleontologic work of Cuvier and Alexandre Brongniart (1770–1847) in the Cretaceous and Tertiary strata of the Paris basin revealed a similar zonation of rocks and fossils.

Lamarck and Acquired Characters.—Jean Baptiste de Monet, better known as the Chevalier de Lamarck (1744–1829), was the son of a Swiss army officer and began his own career in the French army. After being severely wounded, however, he briefly studied theology and then medicine and became interested in science. His first work in botany brought him into contact with Buffon. In 1778 he was appointed custodian of the Paris botanical gardens, but after a few years, his interests shifted to the study of invertebrate animals and, in 1804, he became professor of zoology. Lamarck was handicapped in his work by lack of private means but he was gifted with powers of rapid and accurate observation and wrote easily and well. He became blind in 1819, withdrew from active life, and his later writings were dictated to his daughter.

Lamarck is known principally for presenting a complete theory of evolution. This closely paralleled one previously propounded by Erasmus Darwin (1731–1802) but appears to have been developed independently. Lamarck's thinking was greatly influenced by both Aristotle and Buffon but he broke away from their ideas. He did not believe in the inherent guiding purpose of Aristotle that gave rise to more and more perfect beings. Instead, new structures and new adaptations resulted from the needs or wants of organisms, and structures or organs increased or decreased in efficiency or size according to whether they were used or not. The characters thus acquired by individual organisms during their lifetimes were preserved and inherited in some degree by their descendants. Unlike Buffon, Lamarck considered that changes of environment did not directly produce changes in organisms.

Lamarck was essentially a uniformitarian. Much time was required to permit evolution to proceed by a myriad of minute stages. Such gradual change, he realized, necessitated the conclusion that species are not stable entities. This led him to a consideration of the details of zoologic relationships. His knowledge of invertebrates, which was unrivaled at this time, indicated that evolving organisms had not radiated from a single

central stem but ramified outward in numerous directions, producing a branching structure like a great tree. This conclusion differed fundamentally from the single advancing scale of Aristotle, whose idea had been shared by most later naturalists.

Lamarckism, in spite of its logical structure, attracted few adherents. It was strongly opposed, and even ridiculed by Cuvier, one of the most influential men in France, and by most naturalists in other countries. The scientific community was not ready for a theory of evolution. Lamarck's ideas were not revived until nearly half a century had passed.

Cuvier and Vertebrate Paleontology.—Léopold Chrétien Frédéric Dagobert Georges Cuvier (1769–1832) was born in a part of Germany that later became French and was educated at Stuttgart. The works of Buffon, which he read as a young man, attracted him to the study of nature. After moving to Paris, he became successively professor of natural history and of anatomy. He was an able and widely popular man and, in addition to scientific activities, was drawn into public administration. He was appointed Councilor of State, Chancellor of the Imperial University, and later was created Baron and made a Peer of France.

Although Cuvier raised the objective study of comparative anatomy to the status of a useful science and established paleontology as prehistoric zoology, most of his theoretical conclusions show him to have been an extreme reactionary. This is strange because he started his scientific career with ideas similar to Buffon's and then steadily regressed. His opposition to Lamarck's theory largely was responsible for its rejection by most contemporary naturalists.

Curvier also contributed significantly in the field of Tertiary mammalian paleontology. His knowledge of the comparative anatomy of vertebrates far exceeded that of all contemporaries. This led to his formulation of the principle of the correlation of parts. He believed that from the observation of one part of a skeleton, he could predict the nature of its other parts, and in this he was remarkably successful. Comparison of fossils with modern species convinced him that many represent extinct forms of life. Also, he concluded that the ancient animals lived in the region where their remains now are found and, by their nature, provide evidence with respect to climatic variations of the past.

Differences in the fossils characteristic of successive stratigraphic zones were interpreted by Cuvier as evidence of a succession of catastrophies that resulted in the extinction of whole faunas. The last of these, which occurred some 5000 to 6000 years ago, was the biblical flood. Cuvier believed in the immutability of all organic species and denied any connection between fossil and living animals. For a time he maintained that each catastrophic extinction was followed by the special creation of a whole new fauna, but later he relinquished this idea.

Cuvier's conclusions were accepted enthusiastically, particularly in France and England, and served to retard progressive biologic and paleontologic thought for more than a generation.

Brongniart and Paleobotany.—Fossil plants, observed since very ancient times, have not posed such obvious problems as have fossil marine animals because plants are native to the land and require no special explanation to account for their occurrence. Consequently, fossil plants were less commonly commented upon by the early naturalists. Not until specimens were recognized as being distinctly different from modern local floras was much attention paid to them. One of the first botanists to note such differences was Antoine de Jussieu who, in 1718, concluded that Carboniferous specimens had been brought to France from either the East or West Indies by the flood.

A century later, plant fossils became the subject of special study in both Germany and France. Kaspar Maria, Count von Sternberg (1761–1838), and Adolphe Théodore Brongniart (1801–1876) independently attempted to integrate fossils into the system of classification of modern floras and laid the groundwork for systematic paleobotany. Brongniart's work was particularly important because it was more extensive. He was the son of Alexandre, who collaborated with Cuvier, and the younger Brongniart adhered to Cuvier's theories in general. He recognized the progressive development of floras from ancient to modern times but believed that changes had been caused by cataclysmic happenings. These early studies were based only on gross mor-

phology but soon afterwards attention was directed to the microscopic features of wood and other structures.

The few evolutionary botanists generally were unable to apply Lamarckian principles to plants. These organisms have no nerves, muscles, or volition and consequently could not, through their own efforts, effect change in structure. Plant evolution, therefore, commonly was considered to have been induced by climatic conditions according to the theory of Buffon.

Lyell and Historical Geology.—Sir Charles Lyell (1797–1875) was the eldest son of a well to do Scotch family. He was trained for the law but an early interest in nature, and particularly geology, led to a career in science, and he became the most influential geologist of his generation. He taught only briefly and was mainly a publicist who devoted most of his life to writing and travel. His *Principles of Geology*, published in three volumes between 1830 and 1833, was the first modern text book of geology. It appeared in many later editions and was translated into several foreign languages.

Lyell was Hutton's most influential follower. He presented the principle of uniformitarianism effectively, and almost single handed won the battle against catastrophism that was so strongly entrenched, especially in England. He converted geologic history for the first time into a rational and understandable account of the slow development of the earth. He opposed the belief that organisms had achieved progressive perfection by a process of successive extinctions and recreations. He emphasized the incompleteness of the preserved geologic record, which accounts for the distinctiveness of the series of observed faunas and floras. He explained that, over the course of time, some species migrating from distant regions displaced and perhaps caused the extinction of their predecessors.

Strangely, Lyell was not an evolutionist and failed to apply his uniformitarian principles to paleontology. He understood the struggle for existence among organisms and realized that competition between species might result in the extinction of less favored kinds. Competition within a species, however, also resulted in the elimination of the less fit varieties, and because species are adapted to their environments, this guarantees the survival of the standard type. Thus, a mechanism is provided for the extermination of some species but nature provides no means for the production of new ones. Lyell opposed Lamarckism and he not did become a convert to Darwin's views until late in life.

Forbes and Ecology.—All observant persons have noticed how organisms, and particularly animals, are adapted to their environments and their peculiar ways of life. This was commented upon by the ancients and it was one factor leading Aristotle to the belief that a guiding principle was responsible for the progressive perfection of all living things. Much later, western European naturalists saw in adaptation convincing evidence that an intelligent creator had planned all details of the organic world. Buffon, however, presented the idea that adaptation resulted from changes in climate and kinds of food which directly affected all plants and animals.

Ecology, or study of the relations of organisms to their environments, began with the work of Edward Forbes (1815–1854). This versatile English naturalist studied medicine but became successively a botanist, zoologist, and paleontologist. Observations in the Mediterranean region revealed to him that organisms occur in characteristic associations related to physical environments. He recognized a series of biologic provinces in the Aegean Sea related to depth and other local factors. Later, he applied these principles to comparisons of the modern and fossil faunas and floras of the British Isles in an attempt to understand the geologic changes that have occurred. Similar studies were made by the Swiss paleontologist, Jules Marcou (1824–1898), who was concerned with the life of the Jurassic ocean that formerly covered much of Europe.

Paleoecology has developed very slowly because of the great complexities involved. Marine conditions, particularly, are difficult to observe and to evaluate, and consequently they are relatively little understood. Much useful information applicable to such studies has been gathered in the present century by marine biologists concerned with the feeding problems of commercial fishing grounds.

Owen and Archetypes.—Sir Richard Owen (1804–1892) was a comparative anatomist second only to Cuvier under whom he

studied. Like so many naturalists of a century or more ago, he was trained in medicine. Most of his work was done in vertebrate paleontology and he became director of the British Museum of Natural History.

Owen was an evolutionist only to a limited degree. Even after the general acceptance of Charles Darwin's theory, he adhered to ideas that originated with the ancient Greeks and resembled Buffon's to some extent. He believed, for example, in a creative directing power responsible for the development of all living things. He also held that many modern species were produced by the degeneration of older and more perfect forms. His most interesting idea was that the ancestors of modern species could be reconstructed by generalizing the characters of these species in such a way that all individual peculiarities are eliminated.

Owen's concept of archetypal forms has been popular with some later paleontologists. Cope built upon it his theory of the survival of the unspecialized because he believed that specialization led inevitably to extinction.

D'Orbigny and Stages.—Alcide Dessaline d'Orbigny (1802–1857) developed an early interest in zoology and paleontology. As a young man, he was sent on a collecting expedition to South America by the Paris Museum. He returned with much material of varied scientific interest upon which he published a comprehensive report. His later work was mainly paleontologic and geologic, and he became professor of paleontology at the museum.

D'Orbigny was a pioneer in the study of foraminifera and contributed importantly to paleontology in other ways. He was a follower of Cuvier's catastrophic theory and believed that every geologic age was sharply set off from others by the distinctiveness of its fossils. each species being separately created. Therefore, he concluded that stratigraphy can be based wholly on paleontology. From his study of the fossils, he recognized six great geologic periods (termed terrains) and subdivided the strata of the first five into 27 stages. D'Orbigny's knowledge of Mesozoic paleontology and stratigraphy was detailed and extensive and his stages, particularly in the Jurassic System, proved so useful in organizing stratigraphic data and for correlation that many of them were adopted by later geologists with only minor changes and they are still in use today.

The concept of stages, as time defined stratigraphic subdivisions identified by their fossils, has been familiar to European geologists for many years. In America, somewhat similar subdivisions commonly were termed groups. Until about 1940, adequate distinction was not made between lithologic groups of strata, whose age may vary from place to place, and time defined stages, which are not necessarily consistent lithologically. Confusion in this respect has not yet been eliminated entirely, and it has resulted in some troublesome inaccuracies and disagreements concerning correlation.

Hall and Invertebrate Paleontology.—Invertebrate fossils have been much more extensively collected and studied by more persons than vertebrates or plants because of their wider distribution, commoner occurrence, and greater stratigraphic usefulness. After William Smith's time particularly, increasing attention was devoted to them and an extremely diverse and scattered literature accumulated. Among the invertebrate paleontologists of the nineteenth century, two stand out above almost all others because of the comprehensiveness, excellence, and volume of their work.

James Hall (1811–1898) was born in Massachusetts, studied at the Rensselaer Institute of Troy, New York, the first nonclassical college established in the United States, and taught chemistry there for a short period. When the New York Geological Survey was organized in 1836, he was appointed assistant to Ebenezer Emmons. The next year, Emmons withdrew and Hall was placed in charge of work in the western part of the state. The report of the Survey was published in 1842–1843 in four volumes of which Hall's was the most comprehensive and complete. Thereafter, he became director of the Survey and of the State Museum, a position held for the remainder of his life. Hall devoted most of his energy to collecting and describing Paleozoic fossils. He was temporarily engaged to organize surveys and act as state geologist in Iowa and Wisconsin, and specimens came to him from many other sources. His publications consist of 13 large quarto volumes issued by New York State

and innumerable other articles. These have been an indispensable source and foundation for most later Paleozoic paleontology in the United States.

Joachim Barrande (1799–1883) was trained as an engineer. He left France as a political refugee and settled in what is now Czechoslovakia. There, he became tutor to Prince Henrie de Chambord and later served as administrator of the prince's property. He developed a deep interest in the geology and paleontology of the Bohemian basin and amassed one of the most magnificent collections of Paleozoic fossils ever made by a single man. These he described in 22 large quarto volumes, financing much of the work himself. Barrande's publications bear the same importance to Paleozoic paleontology in Europe as Hall's do in America and, perhaps even surpass them in thoroughness and detail.

MIDDLE SCIENTIFIC PERIOD

Darwin and Natural Selection.—Charles Darwin (1809–1882) occupies a unique position in the history of biologic thought. Although the publication of his *Origin of Species* in 1859 marks a transition from the archaic to the modern in biology, this book presents no basic new idea. Darwin's genius lay in perceiving the implications of several older concepts, combining them in a convincing way, carrying them to their logical conclusions, and presenting such a vast array of evidence and close reasoning that these conclusions could not be contested easily. Also, he was fortunate in writing at a time that was ripe for an integrated and materialistic theory of evolution—Lyell had paved the way with his uniformitarian geology—and in inspiring a small group of enthusiastic and aggressive followers.

At first sight, Darwin seems a most unlikely man to have accomplished what he did. He was the son of a well to do doctor and the grandson of Erasmus Darwin, also a physician. At this domineering father's insistence, he studied first medicine and then theology, but showed no interest or aptitude for either. His appointment in 1831 as naturalist aboard the Beagle, by influence of his professor of botany at Cambridge, was the event that shaped his life. The Beagle, a small British naval vessel, was about to set sail on a surveying voyage around the world. Darwin's father opposed this venture but finally gave consent reluctantly. The captain's approval was granted mainly because Darwin was a "gentleman."

During the five years that he accompanied the Beagle, Darwin studied, among many other things, the plants and animals of the Amazon region, vertebrate fossils collected in Argentina, and life of the Galapagos Islands. These particularly provided the material that started him thinking about evolution. Darwin's contemplation of this subject continued for more than 20 years and his publication on it finally was forced only by the fact that Alfred Wallace independently arrived at almost identical conclusions.

In its essentials, Darwin's theory had three bases: (1) The variability of species—this was well known to most biologists and had been employed by breeders to produce new domestic strains. (2) The struggle for existence—Malthus' *Essay on Population*, published in 1798, explained how human population tends to increase faster than food supply and leads to misery. The reproductive capacity of all wild races also greatly exceeds that necessary to perpetuate existing species. (3) The selection of the fittest—competition among all organisms results in the elimination of the weakest individuals whereas the stronger ones survive and produce more offspring. This principle had been applied in a vague way to natural populations of animals and plants by several biologists and more directly by the geologist, Lyell.

Both Darwin and Wallace drew the logical conclusion: The varieties selected by nature for perpetuation possess structures, functions, or habits that confer some advantage upon individuals. Variation is random and the favored individuals differ in some way from the population norm. Small modifications in characters progressively alter the nature of a population, and differences accumulate until finally a new species has developed. In a similar way, competition results in the expansion of superior species at the expense of inferior ones which may be driven to extinction.

The process of natural selection accounts for the elimination of less fit organisms but

it does not explain how or why new and more advantageous varieties arise. Darwin in complete ignorance of genetics, accepted with some reservations the ideas of both Lamarck and Buffon. He believed that the characters of individuals changed because of the use or disuse of parts, and that environment, particularly climate and food, achieved subordinate results. In order to account for the inheritance of characters so acquired, he assumed that the germ cells include contributions derived from all parts of a mature organism, as suggested by Buffon. During his lifetime, Darwin leaned more and more toward these aspects of Lamarckism.

Mivart and Saltation.—An objection repeatedly directed against evolution, effected only by natural selection, is that such a mechanism does not explain the incipient development of structures that are useles until they have been fully formed. The wings of birds and the eyes of vertebrates commonly have been cited as examples. This objection is reinforced by the fact that intermediate stages connecting well marked differences in specialized structures rarely have been observed.

St. George Jackson Mivart (1827–1900), one of Darwin's principal antiselectionist critics, argued along these lines with considerable skill. Many persons have observed that the appearance of one new important character almost invariably is accompanied by others correlated with it. Such a change in organization is complex and it is inconceivable that this could have occurred by chance alone. Therefore, the conclusion must be drawn that some force or tendency inherent within the organism has guided its development, and new species probably appeared abruptly and fully formed by sudden leaps or saltations deviating importantly from the ancestral type.

This view was met by counter arguments. Most importantly, it was pointed out, two identical sports of opposite sex must have appeared simultaneously in close proximity to initiate the breeding line of a new species. Such an occurrence is exceedingly unlikely.

Mendel and Heredity.—The common resemblance of parents and offspring has been observed by everyone, and the atavistic recurrence of traits inherited from a more remote ancestor likewise has been noted since very ancient times. Although the importance of inheritance rarely has been denied, an indication of how it operates was first obtained by Johann Gregor Mendel (1822–1884), an Augustinian monk in part of Czechoslovakia then included in the Austrian Empire.

Mendel conducted extensive experiments in plant breeding and obtained results that mark the beginning of an understanding of genetics. He crossed pure strains of peas and observed the resulting relations of unit characters which were analyzed statistically, For example, he crossed short and tall plants and discovered that the offspring were not intermediate in height as was expected. All were tall. When self pollenated, these second generation plants produced offspring one-quarter of which reverted to the short type and bred true. Another quarter were true breeding tall forms. The remaining half consisted of tall hybrids like their parents.

From these and other similar results, Mendel concluded that every plant possessed paired factors of inheritance, one set of which was derived from each parent. The factors controlling characters such as height were either dominant (tall) or recessive (short). In hybrid plants, the dominant factor masked the recessive one. The paired factors separated in reproduction so that each germ cell of the hybrids possessed a single factor which was either dominant or recessive. These combined according to the laws of chance to produce seeds and therefore the next generation consisted of short, hybrid, and true tall plants in the ratios of 1 to 2 to 1.

This principle of Mendelian inheritance passed unnoticed at the time and was not discovered by botanists until about 35 years later.

Wallace and Zoogeography,—Every naturalist is aware that all kinds of organisms are restricted geographically. Since at least Buffon's time, this fact had been considered in relation to theories concerned with the origin of species and their possible migrations. Alfred Russel Wallace (1823–1913), who with Charles Darwin developed the concept of evolution by means of natural selection, reviewed the present distribution of land animals in considerable detail. He attempted to reconstruct the history of

their migrations since early Tertiary time from their present zoologic and geographic relationships and thus to obtain a more precise understanding of changes in the extent and continuity of land and sea and of climate than can be derived from knowledge of the physical aspects of geology alone.

Wallace was trained as a surveyor and architect but he acquired an interest in botany and entomology and became a professional natural history collector. After an extended trip through the Amazon valley in South America, he devoted eight years to collecting in the East Indies. There, he observed the divergent distributions of mammals and other animals which directed his attention to zoogeography. Wallace believed that every species originated by evolution within a more or less restricted region and then broadened its range to the extent permitted by changing physical geography. Changes also served to isolate parts of formerly widely continuous populations each part of which later evolved independently. Thus, the modern distributions of species, genera, and larger taxonomic groups provide clues to the climate, topography, and communication routes as these existed at more and more remote epochs of the past. Further information is provided by fossils which are particularly useful in indicating whence and in what directions the migrations had progressed.

Haeckel and Phylogenetic Classification.—Darwin's *Origin of Species* was published in six editions between 1859 and 1872. Not only did it create an immediate sensation in Victorian England, but it attracted wide attention in other lands. Particularly, it stimulated the thinking of young men, many of them in foreign countries, who reached maturity between these dates, and a large number of them later contributed actively to the development of evolutionary theory. Before the end of this period, some form of evolution was accepted by most younger scientific men except in France where Cuvier's influence persisted.

Ernst Heinrich Haeckel (1834–1919), the famous German zoologist, was one of Darwin's most stalwart and influential supporters. He was the first consistently to attempt the application of evolutionary theory to the classification of animals. Most previous classifications had been based simply on morphologic similarities and differences without any consideration of possible genealogic relationships. Many features of these classifications proved to be unsatisfactory according to this newer principle, and most later systems followed Haeckel's example in attempting to base classification on phylogeny.

Embryologists had discovered that higher animals, in their early development, pass through a series of stages which, when traced backwards, resemble lower and lower types. This was accepted as evidence substantiating evolution, and the conclusion was reached that each individual repeats the evolution of its race in accelerated fashion. The formulation of this principle or biogenetic law that "ontogeny recapitulates phylogeny," generally is attributed to Haeckel.

Hyatt and Recapitulation.—Application of the recapitulation principle to paleontology was made by Alpheus Hyatt (1839–1902) particularly with respect to cephalopods. His work, and that of several of his most able students, resulted in acceptance of this principle by most invertebrate paleontologists, especially in America.

Hyatt studied at Harvard under Louis Agissiz (1807–1872) who had observed that fishes, in their development, passed through stages resembling earlier and more primitive forms but refused to believe that this is evidence of evolution. Hyatt became professor of zoology at Massachusetts Institute of Technology and assistant in paleontology at the Museum of Comparative Zoology. Much of his research was devoted to fossil cephalopods, particularly Paleozoic forms, and he became the recognized authority in this field of paleontology. He was impressed by the facts that nautiloids seem to have progressed from straight to curved, loosely coiled, tightly coiled, and finally to involute forms, and that ammonoids progressively developed more and more complex sutures. He believed these to be phylogenetic tendencies demonstrating the inheritance of acquired characters. Acceleration of development forced the earlier stages farther and farther backward in ontogeny as more and more advanced features made their appearance at maturity.

Except for his Lamarckian conclusions, Hyatt's interpretations are still considered to be correct so far as some ammonoids are concerned. Others, however, present convincing evidence that new characters appeared first in very early developmental stages and, in descendant generations, persisted longer and longer until finally they became the characters of mature shells. This is the exact reverse of recapitulation. Although recapitulation appears to be exhibited in the growth of many embryos, similar development certainly cannot be recognized in all animals. Part of the fallacy in Hyatt's reasoning lay in his assumption that embryonic and later growth are strictly comparable. In its post-embryonic development, every individual is subject to environmental influences, and natural selection can effect evolutionary change at any stage. It is now well known that some important larval and other immature adaptations involve the modification of structures and habits independently of any changes in the adult.

Cope and Neo-Lamarckism.—A school of Neo-Lamarckians developed rapidly, particularly among paleontologists in America. Its members accepted the principle of natural selection but, in addition, carried Darwin's Lamarckism to extremes. Edward Drinker Cope (1840–1897), the eldest son in a well to do Quaker family of Pennsylvania, was one of the outstanding members of this group.

Cope became interested in animals in boyhood and obtained an extensive and detailed knowledge of comparative anatomy. He became a vertebrate paleontologist by avocation, later was associated with the Hayden and Wheeler surveys in the west, and finally served as professor of geology and mineralogy at the University of Pennsylvania. Throughout his life, much of his collecting and scientific work were supported by his own limited private means.

Like others, Cope recognized that natural selection alone provides no explanation for the appearance of new characters. He attempted to account for evolution by the operation of forces that first originated new structures and then directed their further development. He believed that effort or will on the part of individuals directed nutrition to certain spots and resulted in the beginning of a structure. Thereafter, stimulated by use and superior nutrition, the structure was progressively perfected. Each stage of advancement acquired by an individual was inherited by its descendants.

Neo-Lamarckism has had a history of alternate revivals and eclipses. Cope carried his ideas to almost ridiculous extremes and continued to advocate them long after they generally were considered to have been discredited. Neo-Lamarckism, however, in one form or another has persisted to the present time.

Dohrn and Function.—The relations connecting structures and functions are obvious and have been commented upon by many biologists. Darwin presented several examples but his interpretations were not consistent. For instance, he considered that the beginning of a new structure might occur by chance or it might result from the development of a new functional activity by an old structure. Perhaps this difference is not important and perhaps both are true. The transformation of a fish's swim bladder into lungs has been cited as an example although a reverse relation is considered now to be more probable.

In any case, functional change certainly must exert an important influence on structural development. The principle that such change is the most important driving force in evolution generally is attributed to Anton Dohrn (1840–1909). He was the son of a German entomologist and studied under Haeckel. His main interests lay in the field of marine zoology and he founded the famous biological station at Naples. Since his time, Dohrn's principle has been developed further and it has been accepted by some as the proper explanation for many evolutionary processes.

Zittel and Systematic Paleontology.—Interest in paleontology rapidly increased in the first half of the nineteenth century, stimulated particularly by the work of Smith in England and Cuvier in France. As the number of described species and genera multiplied, more and more need developed for systematic work to bring order out of the investigations recorded in an expanding literature. The first important compilation was by a Swiss paleontologist, François

Jules Pictet (1809–1872) who arranged fossils in a classification similar to that employed for living animals, and this became the model for several later works. Heinrich Georg Bronn (1800–1862), professor at Heidelberg, published an alphabetical list of all known fossil genera and species with bibliographic references and stratigraphic notes.

Before the appearance of the *Origin of Species*, most paleontologists followed Cuvier in considering species to be immutable, and most classifications were simply morphologic. After 1859, however, rapid acceptance of the evolutionary theory occurred and Haeckel's phylogenetic type of classification was approved. Karl Alfred Ritter von Zittel (1839–1904), professor of paleontology at Munich, was the first to present a broad consideration of fossils from this viewpoint. He contributed little to theory but rejected the Neo-Lamarckian interpretations of Hyatt, Cope and others. His exhaustive four volume work on paleontology appeared in German between 1876 and 1893. It characterized all genera of fossils arranged in a supposedly phylogenetic classification and became the standard reference. This was followed in 1895 by a condensed version that was translated and issued in more or less revised form in several other languages.

Further paleontologic studies have increased the number of recognized genera so greatly that no man now is competent to handle more than some restricted group of fossils. Recent comparable compilations, completed or in course of publication, are the work of numerous contributing specialists.

MODERN SCIENTIFIC PERIOD

Weismann and Germ Plasma.—Beginning of an understanding of germ cells and the part they play in the sexual origin of organisms dates back to the time of Leeuwenhoek (1632–1723), and later it became obvious that these cells carry the elements of heredity. Belief in the inheritance of acquired characters necessitated the conclusion that the nature of the germ cells is determined by the whole body of the individual producing them. The idea naturally developed that some sort of tiny particles produced in all parts of the body migrated to and were concentrated in the germ cells. Ideas of this kind dating back at least to Hippocrates (460–370 B.C.), were held by Buffon and elaborated by Darwin.

August Weismann (1834–1914), professor of zoology at the University of Freiburg, investigated insect anatomy, but weak eyes forced him to abandon observational studies and his principal contributions to biology relate to theoretical problems. He viewed the matter of inheritance in a different way. In order to account for the differentiation of structures in ontogenetic growth, he believed that the hereditary determinants contained in the fertilized ovum were gradually sorted out and segregated in those parts of a developing embryo destined to become the completed parts of the mature organism. He suggested that the determinants are highly complex chemical substances contained in those parts of the cell nucleus later termed chromosomes. As division of the ovum occurred, determinants separated and were passed on in progressively simpler associations to all the daughter cells except those that developed into the sex glands. These persisted in unaltered form as the germ plasm that was transmitted essentially unchanged from generation to generation. Some subtle modifications did occur, however, and these account for variation within species and eventual evolution.

Although Weismann's theories were very largely speculative and mainly incorrrect, they mark the beginning of a new era in the studies that developed into genetics. They directed the attention of cytologists to the structures and transformations that occur within cell nuclei and related processes involved in reproduction and the transmission of hereditary traits.

Williams and Biologic Paleontology.—A century or more ago, scientific knowledge was not so extensive but that one person could acquire an adequate understanding of several more or less broadly interrelated fields. Many of the early paleontologists were competent biologists, and most of them obtained a good working knowledge of geology. Neither of these sciences was sufficiently advanced, however, for the full significance of either the fossils or the rocks to be understood. Fossils were considered interesting at that time either because they

represent life on earth in the earlier stages of its history or because they serve to date the rocks of different ages.

As time passed, paleontology, particularly of the invertebrates, drifted away from biology and a gulf developed between these studies that gradually widened. Biologic interests expanded but paleontology remained essentially unchanged. When paleontologists were not engaged in taxonomic studies or in consideration of evolution, their geologic interests led them to build up stratigraphic sequences consisting of units, each identified by some fossil or group of fossils. These units were then correlated from place to place. If a unit at one locality was not matched by a corresponding unit with similar fossils at another. the conclusion commonly was drawn that the latter stratigraphic section was incomplete. Accordingly attempts were made to compile complete sequences on the supposition that the various stratigraphic units wedged in and out.

Henry Shaler Williams (1847–1918), of Cornell and Yale universities, possessed much greater awareness than most other paleontologists of his time that fossils should be considered as once living organisms. His interests directed his attention to the study of invertebrate fossils in their natural associations rather than as individual species. He emphasized the importance of ecologic relations and pointed out that quite different faunas must have lived contemporaneously at different places. This threw a new light on many correlation problems, and Williams attempted to determine the geographic distributions and stratigraphic ranges of the faunas. This viewpoint brought into realistic relations the concept of the stage, as introduced by d'Orbigny, and the undoubted fact that faunas have shifted in accordance with local environmental changes and migrated with the passage of geologic time.

Williams published a book on *Geological Biology*. This now seems quaint and antiquated in many ways but it presented paleontology in general from a much broader point of view than then was the current fashion. Unfortunately, it had little influence on later paleontologic studies.

De Vries and Mutations.—Mivart contested Darwin's theory of the natural selection of small variations and contended that most evolution occurred by sudden jumps in response to some inner force rather than to an environmental pressure. Darwin, of course, was familiar with abrupt saltations, known as sports, but did not consider them important because of rarity and for other reasons. Several later biologists held the view that evolution might proceed either by slow selection or rapid saltation.

Hugo de Vries (1848–1935), a Dutch botanist, provided what appeared to be proof that mutations, as he called them, may actually be important in the evolutionary process. He experimented with the evening primrose that had escaped from cultivation in Europe and gave rise to many and repeated, large scale, true breeding variations. The appearance of these mutants neither could be predicted nor related to environment, and de Vries concluded that they must result from spontaneous, important alterations of the germ plasm. He distinguished between the small variations evident in all species and the large mutations that he considered to be incipient species. Natural selection would act on both. Darwin was concerned with the results of variations that already had appeared. De Vries was interested mainly in the process of variation and mutation.

Mutations now are recognized to be of several different kinds. Most of them are small and result in physiologic changes without immediate structural manifestations. Others are large and obvious. All are subject to the screening action of natural selection and they produce the new noninherited but heritable characters that may result in evident evolution.

Morgan and Genetics.—Knowledge of the behavior of chromosomes at the time of cell division, obtained by cytologists during the latter part of the nineteenth century, and the discovery of Mendel's writings set the stage for the development of modern genetics. W. S. Sutton appears to have been the first to grasp the important theoretical implications of these matters. Experimental work soon followed and genetics rapidly grew into one of the major branches of biology.

Thomas Hunt Morgan (1866–1945) of Columbia University and California Institute of Technology and his followers, working principally with the fruit fly *Drosophila*,

observed clear-cut mutations that confirmed Mendel's results and others that did not. From these, it became apparent that the relations of factors or determinants of heredity, or genes as they now were called, and morphologic characters are much more complex than had been supposed. The gene theory that emerged accounts for these relations by assuming that observable unit characters are controlled by gene assemblages, and that individual genes may affect more than one character. Ingenious breeding experiments were devised that indicated how genes are associated in the chromosomes and where specific genes are located. Thus, the theoretical genes were mapped. Investigations, continuing to the present time, are revealing these relations in greater and greater detail.

Some geneticists now believe that the main problems concerning the fundamental mechanism responsible for heredity and evolution have been solved satisfactorily. According to prevailing theories, heredity is controlled by structure of the chromosomes and the interplay of dominant and recessive characters. Evolution is effected by mutations of several kinds, that alter chromosomal structure, and the operation of natural selection upon the individual organisms that result. If this is so, further understanding of the complex processes involved probably will be gained by biochemists who are investigating the chemical nature of cellular constituents and their reactions on each other. There are, however, other geneticists who are sceptical in various degrees and a few who are antagonistic to these theories.

Wright and Population Genetics.—Perfection of the gene theory of heredity opened the way for the mathematical exploration of evolutionary processes. The long continued studies of Sewall Wright (1889–), professor of zoology at the University of Chicago, have furnished the principal bases for such considerations. These are almost entirely theoretical but the results are of particular interest and significance in paleontology.

Several factors enter importantly into most modern analyses of evolution. Among them are: population size, gene variability, gene exchange rates, mutation frequency, and selection pressure. None can be measured accurately but some can be estimated roughly and the results of arbitrarily chosen values can be investigated with respect to each other. Studies show that, in general, large populations consisting of variable individuals are relatively stable and may be expected to evolve only slowly and adaptively; more rapid and flexible evolution is likely to occur in populations of moderate size; and chance plays an important role in very small populations which may evolve with extreme rapidity or degenerate and become extinct as is more probable.

These conclusions have direct bearing on many evolutionary problems and may explain variability and widely differing rates of evolution, and why intermediate forms and connecting links generally are unknown or very rare in the fossil record.

Simpson and Modern Paleontology.—Contemporary paleontology operates at very unequal levels of accomplishment. Most paleontology still is descriptive and much of this shows little advance over the work of earlier investigators except that it is more detailed and precise. The continued accumulation of factual data is essential for the advancement of paleontologic knowledge but it does not necessarily increase the understanding of paleontology greatly as a branch of biologic science.

Interest and competence in both the geologic and biologic aspects of paleontology have been rare in any individual in recent time. Vertebrate paleontologists and paleobotanists have been interested mainly in certain restricted biologic aspects of paleontology, and the former particularly have sought to decipher evolutionary patterns. Invertebrate paleontologists, on the other hand, generally have been much more concerned with geology because of the practical usefulness of their work in correlation. They have been especially backward in the understanding and application of modern biologic principles to their work and, in a scientific sense, many of them have fallen far behind biologists. Much of the systematic work in all branches of paleontology is highly speculative, largely morphologic, and does little more than reflect individual opinions regarding the more obvious biologic relationships.

George Gaylord Simpson (1902–), of the American Museum of Natural History and Columbia University, has done much

more than most other modern paleontologists to consider fossils within the framework of biologic science. Like other students of the vertebrates, he has concerned himself principally with evolution. This is of great importance because the study of actual evolution is a field in which paleontology is supreme. Paleontology must provide the factual data substantiating evolutionary theory if this ever is to be obtained, and only paleontology can reveal the ancestry and true relationships of living organisms and the geologic history of life.

Another aspect of biology of outstanding importance in paleontology is ecology. Here vertebrates provide less useful material for detailed investigation than do invertebrates and, to a somewhat less extent, the plants. Paleoecology is exceedingly complex and only recently has it begun to attract the attention it deserves. As yet, no paleontologist has arisen whose accomplishments warrant his recognition as an outstanding student in this field. When one does, he probably will represent invertebrate paleontology.

SUMMARY

Paleontology had its origin in the wonder that arose when persons found strange objects resembling parts of living organisms in the rocks. It did not begin to achieve a scientific status, however, until these objects were recognized to be the actual remains of once living things. Thereafter, it has progressed through several stages of development characterized by attention being directed successively to individual specimens, species and their classification, faunas, and finally evolutionary lineages.

The first paleontologic work necessarily was discriminative and descriptive. This may be termed the stage of species making. Each specimen was compared to others and a decision reached as to whether it belonged to a previously described species or a new one. This kind of work is still being done and it will persist as long as fossils continue to be studied. The species that are distinguished are the units with which paleontologists deal and they find application in geology for correlation. Whether or not they are realistic units that have any kind of meaning depends largely upon the knowledge and good judgment of the person who erects them.

The study of species leads to classification. At first the grouping of species into genera and other taxonomic units was wholly morphologic. Evolutionary theory, however, introduced the idea that classification should be based on phylogenetic relationships. Classification, according to this viewpoint, antedated the actual recognition of evolutionary lineages because knowledge was very incomplete, and many conclusions interpreting morphology were mistaken. Gradual transition has occurred, therefore, from purely morphologic to phylogenetic classification and it is still in progress. Improvements will continue to be made as long as new knowledge of fossils is obtained. The study of species also leads to the determination of stratigraphic and geographic ranges. This has direct and important applications in the geologic field to correlation and, in the biologic field, to an understanding of distribution and migration.

Faunal and floral studies involve consideration of individuals and species from the standpoint of both biologic and physical associations and environments. They have progressed from the simple observation and recording of associated species to the study of population relations involving consideration of the numbers of specimens representing species. Studies of this kind find application in the interpretation of facies relations, which are important in correlation and migration, and a better understanding of environments that may throw much light on the nature of some past physical conditions not revealed by the sediments alone.

Most biologic studies converge upon the consideration of evolution which gives meaning to all features of living things. The most fundamental aspects of biology are involved, and all theories offered to account for them must be checked against the fossil record. The working out of evolutionary lineages and the recognition of trends in evolutionary development provide additional knowledge useful in the solution of correlation, distribution and population problems.

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JOURNAL OF PALEONTOLOGY, V. 34, NO. 5, P. 1020–1022, 2 TEXT-FIGS., SEPTEMBER, 1960

TURBINOLIA ROSETTA, A NEW CORAL SPECIES FROM THE PALEOCENE OF ALABAMA

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ABSTRACT—A new coral species, *Turbinolia rosetta*, is described from the Midway group (Paleocene) of Alabama. This is only the second *Turbinolia* reported from Paleocene deposits.

INTRODUCTION

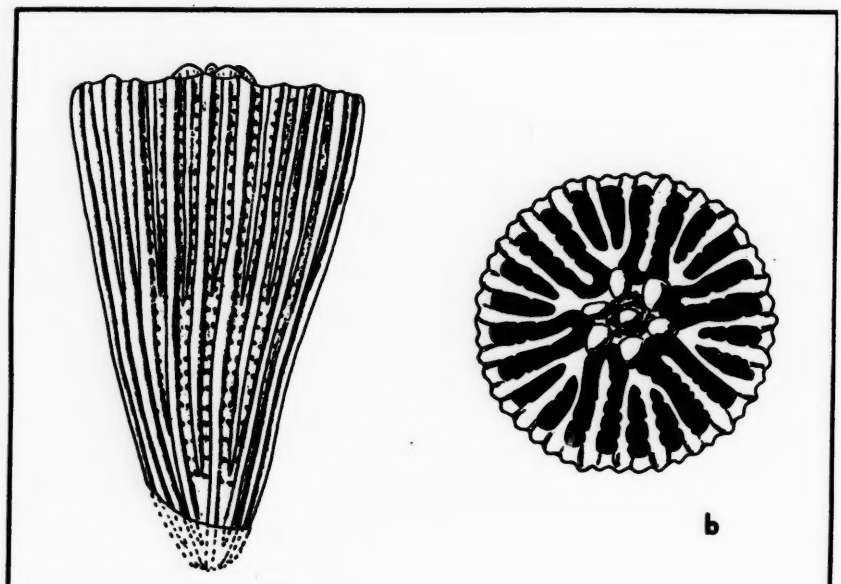
AN EXAMINATION of a Midway sample from the Paleocene deposits of Wilcox County, Alabama, reveals a distinctive new species of *Turbinolia*. This is the second *Turbinolia* species reported from the Paleocene; the first, *Turbinolia midwayensis*, was described by Monsour (1944) from the Clayton formation, Midway group of Mississippi.

The writer is indebted to Dr. Henry V. Howe, who collected the study material, and at whose suggestion the work was undertaken.

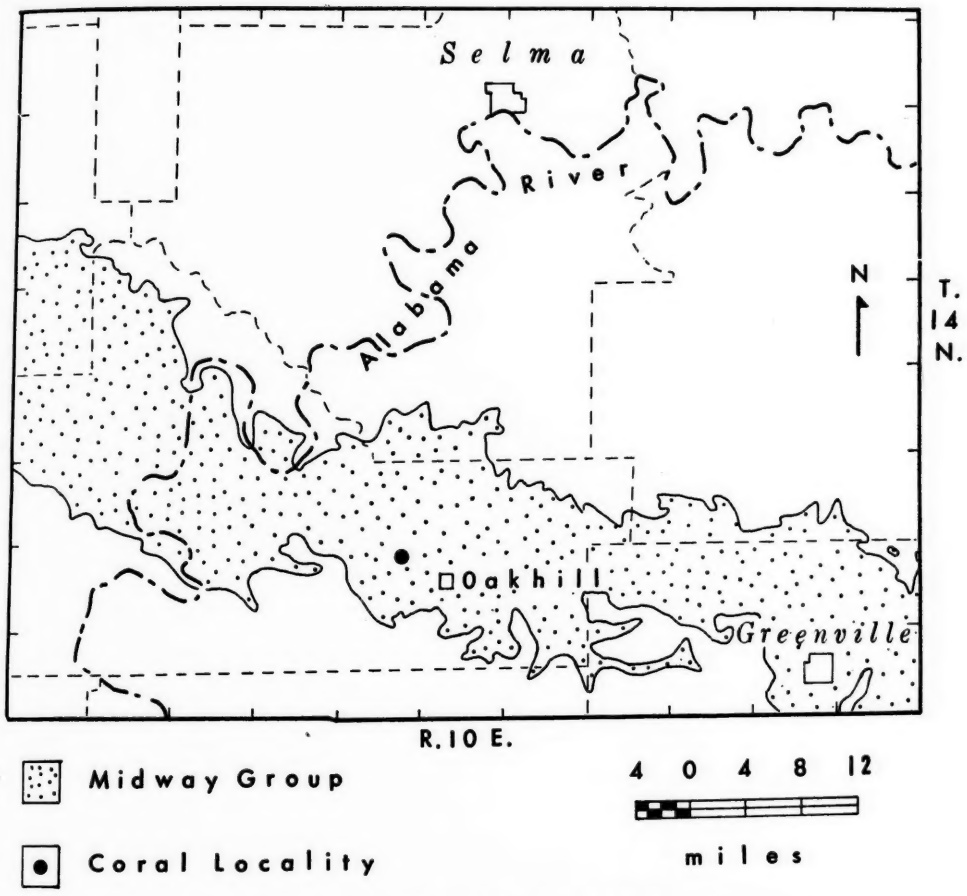
DESCRIPTION

Family CARYOPHYLLIIDAE Gray, 1847
Subfamily TURBINOLIINAE Milne-Edwards & Haime, 1848
Genus TURBINOLIA Lamarck, 1816
TURBINOLIA ROSETTA Howe, n. sp.
Text-fig. 1

Corallum small and conical. Cross section circular. Costae 48 in number, rounded in profile; 24 correspond to the septa and 24 occupy interseptal positions. Septal costae all of the same size; rudimentary costae shorter and narrower. Primary costae pro-



TEXT-FIG. 1—*Turbinolia rosetta*, n. sp. Side view (a) and top view (b), ×16.



TEXT-FIG. *2*—Index map showing type locality of *Turbinolia rosetta*, n. sp. Map data from Mississippi Geological Society (1953).

longed to the apex of the base, secondary to about 0.25 mm. from the base, and tertiary to about 0.75 mm. from the base. From the calicular margin the rudimentary costae become progressively finer terminating about 2.2 mm. from the base. Intercostal furrows perforated by double rows of pores, which become divided into single rows by the rudimentary costae.

Septa somewhat exsert, 24 in number in three cycles. Lateral surfaces of septa granulated with numerous minute spines. Granules do not show any definite arrangement. Halfway from thecal wall to columella, septa of third cycle curve and fuse solidly to primary septa except for a series of pores along the inner margin.

Remarks.—The following features distinguish this species from *Turbinolia midwayensis* Monsour: costae are thicker, more rounded, and not as prominent; tertiary costae are longer; intercostal furrows are shallower; rudimentary costae are better developed; lateral surfaces of septa contain more numerous spines; and the rosette pattern of the columella is unique.

This species differs from *Turbinolia claibornensis* Vaughan (1900, pl. VI, fig. 14 to 16b) in that the latter is larger, lacks a rosette columella, and has acute delicate costae.

Type locality.—Study material was collected from bed 5 of the Matthews Landing marl member, Porters Creek formation,

Midway group at a creek exposure about 200 feet off Alabama Highway 10, four miles west of Oakhill, Alabama (text-fig.2). A section description is given by the Mississippi Geological Society (1953, p. 33).

Type.—Holotype, diameter of calyx, 2.3 mm.; height of corallum, 3.8 mm. Holotype is deposited in the Louisiana State University Geology Museum, number 7084.

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JOURNAL OF PALEONTOLOGY, V. 34, NO. 5, P. 1023–1026, 1 TEXT-FIG., SEPTEMBER, 1960

SILURIAN EURYPTERIDS FROM WEST VIRGINIA

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ABSTRACT—Eurypterids have been reported at only four places in West Virginia. A new eurypterid horizon is described at one of these localities. At least four genera are present in the Willis Creek formation. A single fragment of an *Eurypterus* may have been obtained from the overlying Tonoloway formation. The prosoma of *Dolichopterus cumberlandicus* Swartz is redescribed on the basis of a newly discovered specimen.

INTRODUCTION

EURYPTERIDS have been found in most parts of the Salina basin (Cayugan of northeastern United States), but the majority of the species are known from a single locality or from a very limited geographic area. Moreover, several of these species are based entirely on holotypes which show only a small part of the animal. Some such "species" may be different parts of a single form. In an effort to collect more nearly complete specimens and to increase our knowledge of the stratigraphic and geographic range of the Silurian Eurypterida, the writer has undertaken a search for previously described localities as well as for new occurrences. This paper is a summary of the available information pertaining to the stratigraphic and geographic distribution of eurypterids in West Virginia.

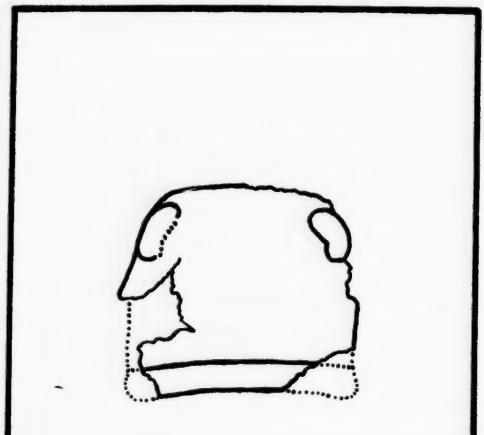
LOCALITIES

Elkhorn Mountain.—Tilton and others (1927, p. 262) first reported eurypterids in the Cayugan strata of West Virginia. These were fragments identified as "*Eurypterus* sp." found at the top of the "Rondout" (Wills Creek) in Hardy County. Kjellesvig-Waering (1950) revisited the locality and subsequently described a new species of *Hughmilleria*, *H. bellistriata*, which he collected from this formation. The *Hughmilleria* was associated with indeterminable species of *Pterygotus*, *Eurypterus*, *Lingula* and marine ostracodes.

The writer searched for this locality in 1959. According to Tilton and others (*loc. cit.*), the original specimens were found along a road leading up the east side of Elkhorn Mountain "0.25 mile northwest of Bass Post-Office." The same authors (p. 284) also referred to a basal Keyser (Devonian) exposure "$\frac{1}{4}$ mile northwest of Bass Post-Office" and a McKenzie (Niagaran) locality "0.3 mile northwest of Bass" (p. 257), both along the same road as the eurypterid discovery. According to the accompanying geologic map (Tilton *et al.*, 1927, map IV), the entire area in question is within the "Bossardville" (Tonoloway) formation. Kjellesvig-Waering (1950, p. 227) indicated that his specimens were found along this road "one third mile northwest . . . of the church at Bass." (There is no material difference whether measurements are referred to the church or to the post office.)

The section exposed along the road in question shows steeply dipping beds of the Wills Creek and most or all of the Tonoloway. The precise boundary between these formations is not easy to fix at most exposures (*cf.* Swartz *et al.*, 1923, p. 49–50), and in view of the vague, contradictory information as to the eurypterid locality, many fruitless hours were spent searching the road cut.

The road follows a small stream. Approximately 2,136 feet (all distances paced) up the mountain from Bass, the road fords the stream and continues parallel to the south side for an additional 1,398 feet, where there is the first of several hairpin switchbacks. By walking directly to the stream from this switchback, one can arrive at the top of a small asymmetrical anticline in the Wills Creek formation. This structure is 204 feet downstream from the top of the Williamsport (Bloomsburg) sandstone which creates a prominent falls in the stream where it too stands up in an asymmetrical anticline. The intervening section is intricately corrugated, and was not measured in detail. However,



TEXT-FIG. *1—Dolichopterus cumberlandicus* Swartz. Mold of prosoma and first tergite from upper part of the Wills Creek formation at Cedar Cliff, West Virginia, ×1. Chicago Natural History Museum PE 6131. Reconstruction of genal angles based on paratype figured by Swartz *et al.* (1923, pl. LXVII, fig. 1).

the stratigraphic distance above the top of the Williamsport does not exceed 30 feet and is probably less.

In the bed of the stream at the point indicated, there is a half-inch bed of very dark gray limestone which contains *Hughmilleria bellistriata*, *Hughmilleria* n. sp. and leperditiid ostracodes. This is separated from the underlying and overlying two-inch beds of limestone by thin beds of dark, unfossiliferous shale. The lowest limestone contains *Hughmilleria* n. sp. and ostracodes. The highest of the three limestone beds contains the same forms as well as *Pterygotus* (*Acutiramus*) *perryensis* Leutze and *Lingula* cf. *L. semina* Ruedemann. All the eurypterid fossils are disarticulated fragments preserved as graphitic films covering molds and casts which retain the relief of the original parts. Nine prosomas of *Hughmilleria bellistriata*, two of *Hughmilleria* n. sp., and one of *Pterygotus* were collected in addition to other fragments of these genera. The specimen of *P. perryensis* is almost identical in size to the holotype of the species. Curiously, all except two of the prosomas were found in an inverted position, concave side up. The majority of the ostracode valves in the same beds are concave down. The parts of *Hughmilleria bellistriata* and *Hughmilleria* n. sp. are all fragments of small individuals; the largest was probably less than 10 cm. in length.

This occurrence of eurypterids in the stream bed at Bass is significant for several reasons. First, it can be precisely located stratigraphically by the adjacent exposure of the Williamsport sandstone. Secondly, Tilton and others (1928) and Kjellesvig-Waering (1950) indicated that their specimens came from the upper part of the Wills Creek formation. Evidently the writer's locality constitutes a new eurypterid horizon. Thirdly, the only specimen of *Pterygotus perryensis* known heretofore was found in the Tymochtee dolomite of southern Ohio. The meagre, non-diagnostic fauna previously reported from the Tymochtee had made its correlation with Cayugan formations of the Appalachian region difficult. The occurrence of *P. perryensis* in the lower Wills Creek and middle or lower Tymochtee is suggestive, though not conclusive evidence for correlation of the respective units.

Knobly Mountain.—Swartz (1923, p. 717–718) described *Dolichopterus cumberlandicus* from the upper part of the Wills Creek formation of West Virginia. He indicated (p. 718; 777–778) that some specimens of *D. cumberlandicus* were obtained from Riverside, West Virginia. Whereas the precise locality and section at Cedar Cliff were given, (p. 127–129), no details about the Riverside locality were published. Riverside is a station on the Western Maryland Railroad about 1.2 miles southeast of Cresaptown, Maryland. Presumably the eurypterids were found at an exposure of the Wills Creek formation 1.05 miles southeast of Riverside, where the Baltimore and Ohio Railroad enters a tunnel in Knobly Mountain. This would be about 2.9 miles south of the Cedar Cliff section, which is also at the foot of Knobly Mountain. Swartz *et al.* (1923, p. 44) implied that the eurypterids at Riverside and Cedar Cliff were found in the same stratigraphic position. The section at the place indicated is essentially the same as the one at Cedar Cliff.

One of the Riverside specimens (Swartz *et al.*, 1923, pl. LXVII, fig. 3) was recognized as an *Eurypterus* by Kjellesvig-Waering (1958, p. 1134–1135) and has been described as a new subspecies, *Eurypterus remipes swartzi.*

Two specimens of the prosoma of *Dolichopterus cumberlandicus* were figured (pl. LXVI, fig. 3; pl. LXVII, fig. 1). The first of these is badly distorted, the right anterolateral corner having been pushed obliquely towards the left posterior. The other is incomplete, lacking the anterior margin, which Swartz reconstructed as a smooth curve (pl. LXVII, fig. 1). Presumably the reconstruction was based on the left half of the specimen portrayed by figure 3 of the preceding plate. Although the left half of that specimen was apparently undistorted, it must have been bulged by compression of the opposite side. This is demonstrated by a specimen recently collected by the writer from the eurypterid bed at Swartz's Cedar Cliff locality. It consists of a flattened but otherwise undistorted prosoma of *D. cumberlandicus* with the first tergite attached (text-fig. 1). The anterior margin is abruptly angulated just anterior to the compound eyes, but is essentially straight rather than curved throughout the rest of its length. The specimen shown in figure 1 (Swartz *et al.*, 1923, pl. LXVII) lacks very little of the prosoma, and the outline of that specimen is much closer to the original outline than Swartz's reconstruction is. The new specimen shows that *D. cumberlandicus* is very similar to eurypterids collected from the lower part of the Syracuse formation in central New York state. The New York specimens are currently under study by the writer.

Keyser.—The only other eurypterid locality in West Virginia known to the writer was mentioned by Reger (1924, p. 382–383; 760), who recorded a fragmentary prosoma of *Eurypterus* sp. found near Keyser. As far as can be ascertained, this specimen was collected from the Tonoloway formation. The fossils in the same collection seem to be Tonoloway forms (*loc. cit.*, p. 760), and this genus is not unknown in the Tonoloway formation (*E. remipes flintstonensis* Swartz from Martin Mountain, Maryland). It is, however, possible that the specimen was obtained from the same zone of the Wills Creek formation as those from Cedar Cliff, where the eurypterids are found only 11 feet below the formational contact. Eurypterids are so rare in most beds, even within the Upper Silurian, that the discovery of a specimen at Keyser, approximately 13 miles south of Riverside, prompts the suggestion that it may have been obtained from the same stratigraphic zone as those found at Riverside and Cedar Cliff.

SUMMARY

The following eurypterids have been reported in West Virginia:

Hughmilleria bellistriata Kjellesvig-Waering; lower part of the Wills Creek and upper part of the same formation at Bass. This may be the form Swartz *et al.* (1923, p. 716–717, pl. LXVI, fig. 2) designated "*Hughmilleria* sp. *cf. shawangunk* Clarke and Ruedemann," obtained from the Wills Creek formation at Cumberland, Maryland.

Hughmilleria n. sp.; lower Wills Creek formation at Bass.

Pterygotus perryensis Leutze; lower Wills Creek formation at Bass. This species is also known from the lower Tymochtee dolomite of southern Ohio.

Pterygotus sp.; upper Wills Creek formation at Bass.

Eurypterus remipes swartzi Kjellesvig-Waering; probably from upper Wills Creek formation at Riverside.

Eurypterus sp.; upper Wills Creek formation at Bass; Tonoloway formation (?) at Keyser.

Dolichopterus cumberlandicus Swartz; upper Wills Creek at Cedar Cliff and same (?) horizon at Riverside. A similar form occurs in the Syracuse formation of central New York state.

ACKNOWLEDGMENTS

Mr. Erik N. Kjellesvig-Waering graciously examined some of the newly collected eurypterids and his generic identification of the *Hughmillerias* are gratefully acknowledged. All specimens collected by the writer have been deposited in the Chicago Natural History Museum, no. PE 6131to PE 6151, inclusive.

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A SURVEY OF THE DECCAN INTERTRAPPEAN FLORA OF INDIA

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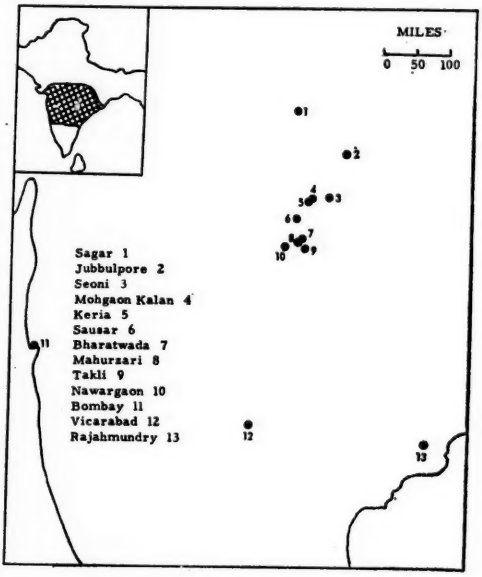
ABSTRACT—The Deccan Intertrappean flora, so far known, is summarized in the present paper. The flora is mostly silicified and often very well preserved, representing the groups Thallophyta (fungi, algae and charophytes), water ferns, conifers and angiosperms with both monocotyledons and dicotyledons. Although at this stage of our knowledge of the Deccan flora, it is rather premature to say anything about the paleoecology, I have tried to draw some tentative conclusions from the fossils so far obtained in the Intertrappean beds.

The age of the Deccan Intertrappean beds has been a controversial matter. It has been possible to give here in brief the various views so far expressed by a number of workers and the present official view of the Geological Survey of India, according to which the age of these beds ranges from uppermost Cretaceous to Eocene.

INTRODUCTION

THE Deccan Intertrappean beds, in which plants and animals are preserved, were deposited mainly in fresh water during the considerable intervals of time which elapsed between successive eruptions of lava which began at the close of the Mesozoic era. These fossiliferous beds are formed by fluviatile and lacustrine deposits intercalated with lava flows and serve as valuable guides to the history of animals and plants which existed during that period. Usually these beds are 2–10 feet thick but occasionally they are only 6 inches in thickness. They are not more than 3 to 4 miles in lateral extent. However, they are fairly regularly distributed throughout the lower and upper traps, being rarely absent for any distance in them. The rocks comprise cherts, impure limestones, and pyroclastic materials and have been recorded from the Godavari, Chhindwara, Nagpur, Dhar, Sagar, and Jubbulpore districts, Hyderabad state and parts of Bombay. The fossiliferous Intertrappean beds are high up in upper traps in Bombay, whereas in Berar and Narbada Valley they occur at a height of 300–500 feet above the base of the traps. The Intertrappean localities, which have so far yielded a fine assemblage of flora, are Mohgaon Kalan, Keria, Sausar, Seoni, Nawargaon, Takli, Mahurjhari, Bharatwada, Jubbulpore, Sagar, and Sitapuri in Madhya Pradesh, Vicarabad in Hyderabad State, Rajahmundry in South India, and Worli and Malabar hills in Bombay (Map 1).



MAP 1—The fossiliferous localities of the Deccan Intertrappean series.

The age of the Deccan Intertrappean series has been a controversial matter. The earlier pioneer geologists like Malcolmson (1837) and Hislop & Hunter (1855) suggested its age as Early Tertiary (Sahni, 1937, p. 465). But in later years W. T. Blanford (1867, p. 159) and others were of the opinion that at least the traps and their in-

cluded Intertrappean beds, around Nagpur and Chhindwara were of Late Cretaceous age. However, T. Oldham (1871, p. 77) believed them to be of Eocene age. The Cretaceous view was later adopted by the Geological Survey of India (Medlicott & Blanford, 1879, p. 331–332; Matley, 1921, p. 162; Holland, 1926, p. 64–88; Wadia, 1926, p. 200). The Cretaceous view was official, until the year 1933, when a comprehensive review of the Intertrappean plants by Professor Sahni showed that the plants had strong Tertiary affinities (Sahni, 1934, p. 134–136; Sahni, Srivastara & Rao, 1934, postscript, p. 27). Since then much evidence has been put forth in support of the Tertiary age by Professor Sahni, his co-workers and others (Rao, 1936, p. 218–223, 1950, p. 32–38; Rao, Narayan Rao & Rao, 1936, p. 157–164; Narayan Rao & Rao, 1935, p. 324, 1937a, p. 389–396; Rao & Narayan Rao, 1939, p. 11,12; Sahni, 1937, 1938 p. 59–65, 1940, p. 12–19, 1941, p. 490, 1943a, p. 91; Sahni & Rode, 1937, p. 165–166, 169; Sahni & Rao, 1943, p. 69,70; Mahabale, 1950b, 1953), and at a discussion held at the Hyderabad-Deccan the Tertiary view was generally adopted (Crookshank and others, 1937, p. 459–471).

In 1938 Fermor (p. 58,59) suggested that the Deccan trap lavas probably commenced at the very end of the Cretaceous period, but were mainly erupted in the Lower Tertiary.

Recently Wadia (1953, p. 302) suggested that from the external evidence, it is quite apparent that the Deccan traps can not be older than the Danian stage of the uppermost Cretaceous, while from the internal evidence of fossil fishes, palms and foraminifers, they cannot be much younger than Eocene. However, Krishnan (1953, p. 52), the late Director of the Geological Survey of India, thinks that the Deccan traps range from uppermost Cretaceous to earliest Eocene in Kathiawar, Gujrat and Cutch, while in the rest of the area these are of Eocene age. This is the present official view of the Geological Survey of India.

HISTORY OF THE DECCAN INTERTRAPPEAN FLORA

The first record of the Deccan Intertrappean plant fossils dates back to the beginning of the 19th century when Coulthard (1829) reported that a number of polished fragments of monocot and dicot woods from the neighbourhood of Sagar were presented to the Museum of the Asiatic Society of Bombay by Captain W. T. Nicolls of the Madras Army. In 1833 Dr. H. H. Spry found the remains of palm trees on a portion of limestone formation at Sagar (Coulthard, 1829). Nicolls published an account of a long fossil stem discovered by Spry. He also dug out a tree from Sagar which was 31 feet long and buried under 4 feet of trap and black soil.

In 1837 Malcolmson reported silicified palms and vegetable matter resembling small fragments of grasses and reeds from Jubbulpore and from the neighbourhood of Sagar.

The next observers of importance were Buist (1851) and Carter (1852). They described fossil plants from Bombay Intertrappeans which consisted of plants like conical bulbous roots; pieces of sub-round, slightly longitudinally striated stems; a segment of a small trunk of dicotyledonous tree with bark; an unsatisfactory piece of palm wood; many small fragments of wood like common bamboo; stems of grasses; two small roundish leaves looking more like leaflets of *Acacia;* some fragmental impressions of flat long leaves, both large and small, with longitudinal striae; an impression closely resembling the stem and flower or seed of a cyperaceous plant, something like *Scirpus lacustris;* seeds like that of *Artabotrys odoratissima* with ruminated appearance of the albumen peculiar to the natural order Anonaceae; and some large seed-pods and like bodies.

The main contribution to the knowledge of the Intertrappean plants was made by Rev. S. Hislop (Carter, 1854) and Hislop & Hunter (1855) who described the flora of the Intertrappean series in Central Provinces particularly in the neighbourhood of Nagpur. The fossil plants, which are from the freshwater formations, are both rare and varied consisting of fruits, seeds, leaves, roots and woods.

Of fruits and seeds there are about 50 species including both monocotyledons and dicotyledons (Carter, 1854, p. 718). Leguminosae has large numbers of representatives

among the dicots including Hedysareae, *Cassia*, *Faboidea* of Bowerbank, a double-seeded fruit resembling the *Xulinosprionites* of Bowerbank and a three seeded fruit. The most abundant order of the monocotyledons is Aroideae? of which there are two genera with compound fruits. One with three-seeded ovaries is exceedingly like a small pine-apple and the other with six-seeded ovaries resembles a mulberry. Next to Aroideae?, the most interesting monocots are palms of which there seems to be two genera, viz., a *Nipadites* (Bow.), and another whose generic identity is not known. Besides there are a large number of seeds and *Chara malcolmsonii*. The fruits are almost all from Takli area.

The leaves and roots described by Hislop also belong to Takli. There are twelve kinds of leaves, of which seven are dicotyledonous and five are monocotyledonous. Roots are five in kind of which three appear to be of aroids with which they are closely associated.

As regards the fossil woods three are of dicotyledonous and two of monocotyledonous type. The former in some cases also retain their bark. These woods probably belong to Takli area.

Recently, work on the Deccan Intertrappean plants was taken up by Professor Sahni, his co-workers and students. Within the past thirty years quite a rich literature and volume of knowledge has accumulated about the Deccan Intertrappean flora. In the present review I would very briefly mention only those fossil plants which are specially interesting or important. However, the adjoining table (Table 1) will give the names of all the fossil plants known so far from the different localities of the Deccan Intertrappean series.

In 1939 Professor K. S. Rao and S. R. Narayan Rao described a rich charophyte flora from the Intertrappean beds of Rajahmundry which consists of nine species identical with the Eocene types of Britain and four new to science. These are *Chara sahnii*, *C. indica*, *C. rajahmundrica*, and *C. sampathi*. From the Intertrappean beds of Sausar, Sahni and Narayan Rao (1943) also described a corticated charophyte branchlet bearing an oögonium with an ellipsoid oöspore and named it as *Chara sausari*.

Narayan Rao & K. S. Rao (1937b) discovered the dasycladaceous alga *Holosporella siamensis* in the Rajahmundry limestone. Pia, Narayan Rao & K. S. Rao (1937a) discussed the stratigraphic significance of the Rajahmundry algal flora and showed that it is characterised by the living genus *Neomeris* and the fossil *Acicularia* which does not extend below the Palaeocene. Accordingly they consider that the Deccan traps were erupted during the Tertiary and Cretaceous periods. They (Pia, Narayan Rao, & K. S. Rao, 1937b; Narayan Rao, K. S. Rao & J. Pia, 1938) also described one species of *Holosporella*, four species of *Neomeris* and a new species of *Terquemella*, *T. lenticularis* from the Rajahmundry beds, and discussed the stratigraphical range of these genera.

In 1934 Sahni and Srivastava (Sahni, Srivastava & Rao, 1934) reported some seed-like bodies as *Sausarospermum fermori* and Sahni and H. S. Rao (1943) described glochidia and massulae of a water fern under a new generic name *Massulites*. Recently Mahabale (1950a) while making a detailed study of the development of the sporocarps in the three species of *Salvinia*, *S. auriculata* Aubl., *S. cucullata* Roxb., and *S. natans* Hoffm., found that the genus *Massulites* of Sahni & Rao represents the hollow massula of some fossil species of *Salvinia* allied to the modern species *Salvinia auriculata*. There is also a strong resemblance between the morphology of the puzzling genus, *Sausarospermum* and the megaspores of *Salvinia auriculata* and some other species. Since then he has also found the vegetative parts of *Salvinia* and suggested a new name, *Salvinia intertrappea*, for it (Mahabale, 1950b). As the fossil species compares most closely with the modern *Salvinia auriculata* growing in Brazil and Cuba, it furnishes a link between the Deccan Intertrappean flora of India and the modern flora of South America. Sahni (1943c) discovered sporocarps of another water fern from the Intertrappean beds and instituted the genus *Rodeites* for such fossil sporocarps of *Regnellidium* type. Recently Mahabale (1956) gave an account of the trends of specialization in the sporocarp and spores in the living and fossil Marsileaceae viz., *Marsilea*, *Pilularia*, *Regnellidium* and *Rodeites dakshini* and

TABLE 1—GEOGRAPHIC DISTRIBUTION OF THE DECCAN INTERTRAPPEAN FOSSIL PLANTS*

Fossil Plants	Localities																		Reference
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
	Bombay (Worli & Malabar hills)	Sitapuri	Jubbulpore	Sagar	Mohgaon Kalan	Keria	Seoni	Sausar	Chhindwara	Pupuldoh Reserve Forest area	Sitabaldi	Takli	Mahurjhari	Bharatwada	Nawargaon	Vicarabad	Rajahmundry	Unknown	
THALLOPHYTA																			
FUNGI																			
Perisporiacites varians Sahni & Rao								XX											Sahni & Rao 1943
Palaeosordaria lagena Sahni & Rao								XX											Ditto
Shuklania Dwivedi					X														Dwivedi 1956
ALGAE																			
Oedogonites Dwivedi					X														Ditto
Halimeda																	X		Rao & Rao 1940
Dissocladella intertrappea Narayan Rao & Rao																	XX		Rao & Rao 1940, 1941
Dissocladella?																	XX		Pia *et al.* 1937*b*
Terquemella lenticularis Pia, Narayan Rao & Rao																	XX		Ditto
Acetabularia?																	XX		Ditto
Neomeris a																	XX		Ditto
Neomeris b																	XX		Ditto
Neomeris c																	XX		Ditto
Neomeris d																	XX		Ditto
Holosporella																	XX		Ditto
Holosporella siamensis																	XX		Rao & Rao 1937*b*
Acicularia																	XX		Pia *et al.* 1937*b*
Filament cf. *Ulothrix*							XX	XX									XX		Sahni & Rao 1943, Mahadevan & Sarma 1948
Filamentous alga							XX	XX											Sahni & Rao 1943
CHAROPHYTA																			
?Gyrogonites medicaginula Lamarck							X	X											Ditto
Chara malcolmsonii Sowerby			X	X			X	X								X		X	Ditto, Carter 1854, Mahadevan & Sarma 1948
C. sausari Sahni & Narayan Rao							X	X											Sahni & Rao 1943
C. wrightii Salter																	X		Rao & Narayan Rao 1939
C. helicteres Brongniart																	XX		Ditto
C. medicaginula Brongniart																	XX		Ditto
C. caelata Reid & Groves																	XX		Ditto
C. vasiformis? Reid and Groves																	XX		Ditto
C. turbinata Reid & Groves																	XX		Ditto
C. strobilocarpa Reid & Groves																	XX		Ditto
C. subglobosa Groves																	XX		Ditto
C. aehlerti Dollfus																	XX		Ditto
C. rajahmundrica Rao & Narayan Rao																	XX		Ditto
C. sampathi Rao & Narayan Rao																	XX		Ditto
C. sahnii Rao & Narayan Rao																	XX		Ditto
C. indica Rao & Narayan Rao																	XX		Ditto
BRYOPHYTA																			
Bryophytic sporogonium					X														Chitaley 1949
PTERIDOPHYTA																			
FILICALES																			
Salvinia intertrappea Mahabale					XX			XX											Mahabale 1950*a*, *b*
Rodeites dakshini					XX														Mahabale 1956, Sahni 1943*c*
Azolla intertrappea Sahni & Rao								XX											Rao 1957, Sahni 1941, Sahni & Rao 1943
GYMNOSPERMS																			
?CYCADALES																			
Gymnovulites Shukla					X														Shukla 1946

TABLE 1—*Continued*

Fossil Plants	Localities																	Reference
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
	Bombay (Worli & Malabar hills)	Sitapuri	Jubbulpore	Sagar	Mohgaon Kalan	Keria	Seoni	Sausar	Chhindwara	Pupuldoh Reserve Forest area	Sitabaldi	Takli	Mahurjhari	Bharatwada	Nawargaon	Vicarabad	Rajahmundry	Unknown	
CONIFERALES																			
Indostrobus bifidolepis Sahni																		×	Sahni 1931*a*
Takliostrobus alatus Sahni												××							Ditto
?Pityostrobus crassitesta Sahni												××							Ditto
Mohgaostrobus sahnii Prakash					×														Prakash 1956*a*, 1959*b*
Dadoxylon deccani Shukla																		×	Shukla 1938
D. resinosum Shukla																		×	Shukla 1944*c*
D. eocenum Chitaley									×										Chitaley 1949
D. chhindwarensis Billimoria																		×	Billinoria 1948
Cupressinoxylon intertrappeum Shukla																		×	Shukla 1942
Spiroxylon intertrappeum Prakash & Srivastava		×																	Prakash & Srivastava 1959
ANGIOSPERMS																			
MONOCOTYLEDONS																			
Nipa hindi (Rode) Sahni					×														Sahni & Rode 1937
Nipadites Bowerbank												×							Carter 1854
Palmocarpon compressum (Rode) Sahni					×														Sahni & Rode 1937
P. (*Iriartites*) *takliensis* Sahni												×							Sahni, Srivastava, & Rao 1934
P. bracteatum Sahni																		×	Ditto
P. spp. Sahni																		×	Ditto
P. insigne Mahabale					×														Mahabale 1950*a*
P. mohgaoense Prakash					×														Prakash 1954
P. sulcatum Prakash					×														Prakash 1959*c*
P. indicum Prakash					×														Ditto
Tricoccites trigonum Rode					×														Sahni & Rode 1937
Fruiting axis of *Tricoccites trigonum* Rode					×														Chitaley 1956, Shukla 1950*a*
Palmostrobus Mahabale					×														Mahabale 1950*a*
Palmoxylon kamalam Rode					×					×									Rode 1933*b*, Shukla 1939
P. hislopi Rode					×														Rode 1933*b*
P. solidum Rode					×														Rode 1934*a*
P. mohgaoenis Rode					×														Ditto
P. invaginatum Rode					×														Ditto
P. sclerodermum Sahni							×								×				Sahni 1943*b*, Shukla 1946
P. (*Cocos*) *sundaram* Sahni				×															Sahni 1946
P. edwardsi Sahni		×	×												×				Sahni 1931*b*
P. nawargaoensis Shukla																			Shallom 1941
P. blanfordi Schenk																		×	Sahni 1931*b*, Schenk 1882
P. liebigianum Schenk											×								Ditto
P. dakshinense Prakash					××														Prakash 1958*b*
P. chhindwarense Prakash					××														Ditto
P. eocenum Prakash													×						Prakash 1959*a*
P. surangei Lakhanpal						×													Lakhanpal 1954
Rhizopalmoxylon penchiensis Rode					×														Rao 1934*b*

TABLE 1—*Continued*

Fossil Plants	Localities																		Reference
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
	Bombay (Worli & Malabar hills)	Sitapuri	Jubbulpore	Sagar	Mohgaon Kalan	Keria	Seoni	Sausar	Chhindwara	Pupuldoh Reserve Forest area	Sitabaldi	Takli	Mahurjhari	Bharatwada	Nawargaon	Vicarabad	Rajahmundry	Unknown	
Cyclanthodendron sahnii (Rode) Sahni & Surange					XXXX														Ramanujam 1959, Sahni & Surange 1934
Floral axis of Cyclanthaceae								X				X X							Mahabale 1950*a*
Sparganium																			Mahabale 1953
†*Viracarpon hexaspermum* Sahni																			Carter 1854, Chitaley 1954, Sahni 1944, Shukla 1944*b*
V. elongatum Sahni												X X							Sahni 1944
Amomocarpum sulcatum Sahni																		XX	Sahni, Srivastava, & Rao 1934
A. affine Sahni																			Sahni 1938
Wood cf. Bamboo	XX				X														Carter 1852, Shukla 1942
Stem and Flower cf. *Scirpus lacustris*					X														Carter 1852
Floral axis of Juncaginaceae					X														Varma 1956*b*
DICOTYLEDONS																			
Sahnianthus Shukla					X														Chitaley 1955, Mahabale & Deshpande 1957, Shukla 1944*a*
Sahnipushpam glandulosum Prakash					XX							X							Prakash 1955
Enigmocarpon parijai Sahni												XXXX		X					Dwivedi 1956, Mahabale & Deshpande 1957, Sahni 1943*a*
Fruit cf. *Hedysareae*																			Carter 1854
Fruit cf. *Cassia*																			Ditto
Fruit cf. *Fabodea* Bowerbank																			Ditto
Fruit cf. *Xylinosprionites* Bowerbank																			Ditto
Seeds cf. *Ariaboxys odoratissima*	X																		Carter 1852
Dryoxylon mohgaonse Rode					XX														Prakash 1956*b*, Rode 1936
Wood cf. *Someralia*																			Varma 1950
Wood cf. *Casurina*																		X	Shukla 1941
Euphorbioxylon krauseli Prakash						X							X						Prakash 1957
Glochidioxylon sahnii Prakash																			Prakash 1958*a*
Alianthoxylon indicum Prakash					XX								X						Ditto
Simaruboxylon deccani Prakash																			Prakash 1959*a*
Simarubaceoxylon mahursari Shallom					XX								XX						Shallom 1959
A dicot wood																			Shallom 1958
Dicotylirhizos sahnii Rao					XXX														Rao 1957
Phyllites mohgaonsis Rode																			Rode 1935
Leaf cf. *Lagerstroemia indica*														X					Shukla 1950*a*, Trivedi 1956
Leaflets cf. *Acacia*	X																		Carter 1852
SPORAE DISPERSAE																			
Spores and pollen grains					X			X											Chitaley 1950*a*, 1951*a*, *b*, Sahni & Rao 1943, Shukla & Chitaley 1948

* After this paper has been sent to press, the following two forms are further known from the Deccan flora: *Palmoxylon* sp. cf. *Phoenix* (Mahabale, 1958). *Aeschynomene tertiarum* (Prakash, 1960).

showed that *Rodeites* is closely related to *Regnellidium*. Thus these *Regnellidium* types of sporocarps establish a further link between the petrified flora of Deccan and the modern flora of Brazil in South America.

Yet another water fern, *Azolla intertrappea*, was described in great detail from both Mahgaon Kalan and Sausar by Sahni (1941) and Sahni & H. S. Rao (1943). In 1957 A. R. Rao made some further observations on the microsporocarps of *Azolla intertrappea*. In 1935 H. S. Rao summarized the fossil history of the Hydropterideae.

Among the gymnosperms, so far known from the Intertrappean beds, are a few conifer cones and woods, besides an ovule probably of cycadean affinity. Of the cones, Sahni (1931a) described in detail three species, viz., *Takliostrobus alatus*, *Indostrobus bifidolepis* and ?*Pityostrobus crassitesta*. These cones belong to the Hislop and Hunter collection of the British Museum. Sahni (1931a) thought that the cones of *Takliostrobus* and *Indostrobus* showed abietinean features with certain peculiarities of their own. Both these cones have since been discussed by Hirmer (1934, p. 48, and 1936, p. 38,40) and Hirmer & Hoerhammer (1934, p. 75). Hirmer considers these genera related to *Cheirolepis* Schimper and *Hirmeriella* Hoerhammer of the Rhaetic-Liassic of Franconia. Florin (1940, 1944), however, does not agree with Hirmer's interpretations of the morphology of their cones and thinks that the true systematic positions of all these genera are yet to be determined.

Recently Prakash (1956a) described an ovuliferous cone from an incomplete specimen discovered from the well-known locality of Mohgaon Kalan. Because of the incomplete nature of the cone it was not possible to show its exact affinities. However, on the basis of some more material of the same cone, Prakash (1959b) has instituted a new genus, *Mohgaostrobus*, which shows close relationship with the family Araucariaceae.

Besides the cones mentioned above, a few conifer woods of *Dadoxylon* have been described from these Intertrappean beds (Shukla, 1938, 1944c; Chitaley, 1949). Recently Prakash & Srivastava (1959) described in detail a new species of the taxinean wood, *Spiroxylon* and named it as *S. intertrappeum*. This wood comes from a new locality discovered near Sitapuri in district Dhar of Madhya Pradesh.

Out of a large number of angiosperms known from the Interrappean beds, palms form a dominant group. They are represented by fruits, stems and roots. Most of these come from the well-known locality of Mohgaon Kalan discovered by Professor Rode (Rode, 1933a) who briefly described two new species of *Nipadites*, *N. compressus* and *N. hindi*. In the same paper he described a trilocular fruit, *Tricoccites trigonum* from the same locality which according to Sahni (Sahni & Rode, 1937) belonged to a palm. In 1937 Sahni, in a joint paper with Rode, re-examined Rode's collection of 1933 and referred *Nipadites hindi* to *Nipa hindi* while *Nipadites compressus* was provisionally placed under *Palmocarpon compressum*. Sahni (Sahni, Srivastava & Rao, 1934) also reported fruits of *Palmocarpon* (*Iriartites*) *takliensis* and *P. bracteatum*. In 1950a Mahabale gave a short description of a palm fruit, *Palmocarpon insigne*, resembling the fruits of modern *Bactris*, *Howea*, and *Pritchardia*. Recently Prakash (1954) described in great detail the fruit of *Palmocarpon mohgaoense* from Mohgaon Kalan. He (1960c) has further reported two new species of *Palmocarpon*, *P. indicum* and *P. sulcatum* also from Mohgaon Kalan. In 1956 Chitaley described in detail the fruiting axis of *Tricoccites trigonum*. However, as regards the affinities of this fruit, nothing is definite as yet.

Sahni in 1931b collected a number of species of palm stems mostly from the Deccan for an exhaustive monograph on palms. Since then a number of palm woods have been described in great detail from the Deccan Intertrappean beds. These are *Palmoxylon kamalam* (Rode, 1933b; Shukla, 1939), *P. sclerodermum* (Sahni, 1928, 1943b; Shukla, 1946), *P.* (*Cocos*) *sundaram* (Sahni, 1946), *P. surangei* (Lakhanpal, 1956), *P. dakshinense*, *P. Chhindwarense* (Prakash, 1958b) and *P. eocenum* (Prakash, 1959a).

In 1933b Rode described *Palmoxylon sahnii* which has been referred to the genus *Cyclanthodendron* by Sahni & Surange (1944, 1950, 1953) because of its clumped habit, peculiar fibrovascular bundles and root structure. These authors have also described the leaf of *Cyclanthodendron sahnii*.

Some further observations as regards its structure have recently been recorded by Ramanujam (1959). This plant forms a link between the Deccan Intertrappean flora of India and the modern flora of South America.

Sahni (1944) instituted a new genus *Viracarpon* for a fruiting axis of six-seeded petrified fruits. He distinguished two new species, *V. hexaspermum* and *V. elongatum* and attributed a possible cyclanthaceous affinity for them. Recently Chitaley (1954, 1958) re-investigated many new specimens of *V. hexaspermum* and placed them near to Pandanaceae and Araceae.

The occurrence of *Sparganium* was recently reported by Mahabale (1953) from the Intertrappean beds of Madhya Pradesh who described root, leaf, stem, inflorescence and fruits from the chert. *Sparganium* being essentially a Tertiary genus, its presence in the Intertrappean beds also supports a Tertiary age.

Sahni (Sahni, Srivastava & Rao, 1934; Sahni, 1938) also reported fruits of the family Zingiberaceae from Mohgaon beds and referred them to two new species of *Amomocarpum, A. sulcatum* and *A. affine.*

The dicotyledons are known by flowers, fruits, leaves, roots, and a number of woods. Of the flowers, so far only two are known. These are *Sahnianthus* (Shukla, 1944a; Chitaley, 1955) and *Sahnipushpam glandulosum* (Prakash, 1955). The flower *Sahnianthus* and its fruit *Enigmocarpon parijai* (Sahni, 1943a; Dwivedi, 1956) show close resemblance to *Sonneratia* and strongly suggest a sonneratiaceous affinity (Mahabale & Deshpande, 1957).

So far only a few dicot woods have been described in detail from the Intertrappean beds. They are *Dryoxylon mohgaoense* (Rode, 1936; Prakash, 1956b); *Euphorbioxylon krauseli* (Prakash, 1957), showing a close resemblance to genus *Bridelia* of Euphorbiaceae; *Glochidioxylon sahnii* (Prakash, 1958a) belonging to the *Glochidion* group of Phyllanthoideae in the family Euphorbiaceae and showing a resemblance to *Glochidion* and *Antidesma; Ailanthoxylon indicum* (Prakash, 1958a) and *Simaruboxylon deccani* (Prakash, 1959a) of the family Simarubaceae, showing close affinity with the modern genera *Ailanthus* and *Simaruba* respectively. The genus *Simaruba* grows in Brazil, Venezuela, British Guiana, and Cuba and the record of fossil *Simaruba* from the Deccan Intertrappean beds once again provides a link between the Deccan flora and the modern flora of tropical South America. Prakash (1960) has also described a new species of *Aeschynomene, A. tertiarum* from Mahurjhari near Nagpur.

Recently Shallom (1958) described a fossil wood from Mahurjhari which shows resemblance to the woods of the families Anacardiaceae and Burseraceae. In 1959 Shallom also instituted a new genus, *Simarubaceoxylon* to include all the fossil woods belonging to family Simarubaceae. In my opinion such names representing heterogeneous families are unfortunate and should be avoided as these will cause confusion. From Mohgaon, Varma (1950) reported a wood which according to him belongs to *Sonneratia.* However, from his description, it appears to me that this wood has nothing to do with the genus *Sonneratia.* Varma (1956a) has further briefly described the same wood in his paper on *Sahnipushpam* deleting some of the characters mentioned in his previous note (Varma, 1950). To me this wood seems to belong to *Dryoxylon mohgaoense,* whose exact affinities are yet to be known.

A dicot leaf known as *Phyllites mohgaoensis* (Rode, 1935) and another leaf (Trivedi, 1956) showing a close resemblance to the leaf of *Lagerstroemia indica* are known from the localities of Mohgaon Kalan and *Bharatwada.*

Besides the above megafossils, a number of fungal mycelia, fungal fructifications, spores, and pollen grains referable to the families Lythraceae, Myrtaceae, Palmaceae, Rosaceae, Betulaceae, and Compositae have recently been recorded (Chitaly, 1950a, 1951a, 1951b).

FLORISTIC CONSIDERATIONS

The Deccan Intertrappean flora is of special interest because nearly all the major groups of the plant kingdom are represented and the plants are mostly silicified, their structure being very often exquisitively preserved. It includes the plant groups thallophytes (with algae, fungi, and charophytes), pteridophyta (filicales), gymnosperms (conifers), and angiosperms with

both monocotyledons and dicotyledons (Table 1). However, the angiosperms and thallophytic forms are most common, while the gymnosperms and pteridophytes are not so well represented.

The Deccan flora, so far studied, consists of about 112 different forms which have been referred to 48 genera representing about 92 recognizable species (Table 1). The rest have been recorded without generic and specific epithet.

Besides, 31 different types of spores and pollen grains have also been described (Sahni & H. S. Rao, 1943; Shukla & Chitaley, 1948; Chitaley, 1950a, 1951a). Out of these, five types of spores belong to fungi, five to pteridophytes, two to gymnosperms and the rest to angiosperms. In addition to these some cuticles, vascular elements, epidermal outgrowths, and a number of other plant fragments are also known.

The common plant fossils in the flora of the Intertrappean beds are palms (represented by their stems, roots, fruits and the fruit bearing axis), charophytes, algal forms, and dicotyledons. The accompanying table will show that the plants are not evenly distributed and equally represented in all the Intertrappean localities. However, the well-known localities of Mohgaon Kalan, Sausar and Rajahmundry (Map 1) have yielded a rich flora in comparison to other localities where only a few forms are known.

The outstanding feature of the small flora of Mohgaon Kalan, is the large proportion of palms (Table 1) which predominate over other plant groups such as dicots, other monocots, conifers and water ferns. However, at Sausar, the flora consists largely of aquatic forms such as water ferns, charophytes and fragments of aerenchymatous tissues presumably of aquatic angiosperms (Sahni & H. S. Rao, 1943). The fungal forms are also common here. Similarly, in the beds at Rajahmundry the flora is aquatic and consists of charophytic and algal forms, which must have lived in brackish waters of an estuary (Sahni, 1940, p. 13).

ECOLOGICAL CONSIDERATIONS

It is obvious from the table that quite rich floras are known from Mohgaon Kalan, Sausar and Rajahmundry which differ from each other in composition. The Mohgaon flora is represented by both land and aquatic forms while at Sausar and Rajahmundry the flora is largely aquatic, although the former is a fresh water flora and the latter is an estuarine flora thriving in brackish waters.

In the present state of our knowledge of the Intertrappean flora, it is rather difficult to state anything definite about the palaeoecology. However, I have tried to draw some tentative conclusions from the fossils so far obtained in the Intertrappean beds.

Mohgaon Kalan (22°1′ N.; 79°11′ E.).—Among the fossil species, so far recorded from this area, the great majority are palms, besides other monocots, dicots, a few water ferns and conifers. It is primarily an angiospermous flora.

The Mohgaon flora is a mixed flora, mixed in the sense that it consists of land, aquatic and marshy forms. The land plants include a number of dicots, palms and other monocots, etc. (Table 1). However, the plants like the fossil *Salvinia* (Mahabale, 1950a, 1950b), the fossil *Sparganium* (Mahabale, 1953), *Rodeites dakshini*, a fossil representative of the monotypic genus *Regnellidium* (Sahni, 1943c), *Cyclanthodendron sahnii* (Sahni & Surange, 1953) related to modern family Cyclanthaceae, growing in shallow waters and estuaries in Brazil (Mahabale, 1950b, p. 411), and a species of *Nipa* (Sahni & Rode, 1937), an estuarine genus, indicate an aquatic or marshy habitat.

The fruits and seeds of *Enigmocarpon parijai* with aerenchymatous tissue are adapted for aquatic dispersal and seem to have been fitted for long immersion in brackish water (Sahni, 1943a). Similarly the fruits of *Tricoccites trigonum* possess longitudinal canals in the fibrous fruit coat which must have helped dispersal in water (Sahni & Rode, 1937).

All these plant remains indicate that the flora preserved in Mohgaon cherts includes land, aquatic, and marsh plants, the aquatic forms inhabiting the stagnant waters of shallow pools, lakes and slow-moving streams. Besides this the presence of petrified fruits of *Nipa hindi* (Sahni & Rode, 1937) which closely resemble the stemless palm, *Nipa fruiticans*, common in Sunderbans and other tropical estuaries at the present day, indicates local estuarine conditions and probably a tropical climate like that of Sunderbans today. Reid and Chandler have shown that all the records of fossil *Nipa* lie

approximately along the shore of Tethys Sea, which probably passed not far north of the latitude of Chhindwara (Sahni & Rode, 1937, p. 167).

Sausar (21°40′ N.; 78°50′ E.).—The Sausar flora is quite different in its composition from the flora of Mohgaon Kalan situated about 50 miles to the north, in the same district of Chhindwara. These represent two different ecological facies of the Deccan Intertrappean flora.

Among the fossil plants from Sausar indicating an aquatic habit, the most noteworthy are the charophytes (Sahni & Narayan Rao, 1943), several forms of algae, a species each of *Azolla* and *Salvinia*, a fossil representative of the monotypic genus *Regnellidium* namely *Rodeites dakshini*, and several kinds of aerenchymatous tissues belonging in all probability to flowering plants (Sahni & H. S. Rao, 1943). All these plants, no doubt, indicate that the flora preserved in Sausar cherts was largely an aquatic one and moreover it inhabited stagnant waters of pools, lakes and sluggish rivers (Sahni & H. S. Rao, 1943, p. 68).

Rajahmundry (17°0′ N., 81°45′ E.).—The plant remains found at this locality consist exclusively of aquatic forms like the Charophyta (Rao & Narayan Rao, 1939) and Algae such as *Acicularia*, *Dissocladella*?, *Holosporella*, *Neomeris*, and *Acetabularia*? etc. (Narayan Rao & Rao, 1940; Pia, Narayan Rao & Rao, 1937b). Both the charophytic and other algal forms indicate an estuarine condition near Rajahmundry.

CONCLUSIONS

The Deccan flora, as now known, consists of a large number of plants representing 48 recognizable genera distributed among about 31 families. It includes 3 fungi, 16 algae, 16 charophytes, 1 bryophyte, 3 ferns, 10 conifers, 38 monocotyledons, and 21 dicotyledons. However, the actual number of botanical species would still be less because some of these forms may represent different parts of the same plant.

The present flora as indicated by the presence of *Nipa* and *Rodeites* (a fossil sporocarp resembling the South American genus *Regnellidium*) probably indicates a tropical climate and the occurrence of the fossil remains of Cyclanthaceae, *Rodeites* and *Simaruba* provides a link between the Tertiary flora of the Deccan Intertrappean series and the modern flora of tropical South America. Although, at this stage of our knowledge of the present flora, it would be rather too early to say anything regarding the trends of migration of these elements but it seems quite likely that these groups, once enjoying a wide and greater distribution in the tropics, seem to be strongly reduced at the present time. However, further extensive investigations are needed to unravel the luxuriant Early Tertiary flora of the Deccan, which would not only contribute to our knowledge of the landscape and of the climate which prevailed in what is now Deccan Plateau, but would also help us to build up the Early Tertiary vegetation of the country.

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ONTOGENETIC VARIATION IN THE CRYSTALLOGRAPHY OF ECHINOID CALCITE

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ABSTRACT—In the coronal plates of some echinoid species, orientation of calcite *c*-axes is a function of growth. In *Hemicentrotus pulcherrimus*, the first formed plates (near the peristome) have *c*-axes that are nearly perpendicular to the plate or test surface; plates of intermediate age (near the ambitus) have axes inclined at an angle of approximately 45 degrees; and the axes of the youngest plates (near the apical system) are again nearly perpendicular. In *Lytechinus variegatus* a different pattern obtains but a gradual change in orientation with growth is again observed. Other echinoid species studied do not exhibit ontogenetic variation in calcite crystallography.

It is suggested that the adaptive value of a given preferred orientation of *c*-axes is related to the organism's light sensitivity. Light will pass through a plate having a tangential *c*-axis more readily than through one having a more nearly perpendicular *c*-axis. Littoral echinoids with tangential *c*-axes commonly cover their tests with debris as a shield against light.

Adaptation to light conditions in shallow water through changes in relative developmental rates (in species like *H. pulcherrimus* and *L. variegatus*) may be the explanation for the evolution of one preferred orientation from another in the geologic past.

INTRODUCTION

IN AN earlier paper by the writer (1959), crystallography of the calcite making up the coronal plates of Recent and fossil echinoids was investigated. It was established by optical means that the phenomenon of mono-crystalline structure in echinoid plates is widespread and that fossilization changes crystallographic orientations only if complete solution and reprecipitation has occurred. Stereographic diagrams relating *c*-axis orientation and test morphology were presented for a series of regular echinoid species. In all cases, strongly preferred orientations were found, and in all but two species there was little variation from plate to plate within a single specimen. With the same two exceptions, each species has either perpendicular or tangential *c*-axes, but never both; that is, the *c*-axes are either perpendicular to the plate or test surface, or tangent to it and aligned longitudinally.

The two species that do not appear to follow the above generalizations are the modern forms *Lytechinus variegatus* (Lamarck) and *Hemicentrotus pulcherrimus* (A. Agassiz). In these, not only are there differences in orientation within a single specimen, but also positions intermediate between the tangential and perpendicular orientations are encountered. The differences appear to be related to test growth.

The present paper reports a more extensive study of *Lytechinus variegatus* and *Hemicentrotus pulcherrimus* and explores the relation between echinoid crystallography and ontogeny.

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POST-LARVAL DEVELOPMENT OF ECHINOIDS

The development of the calcareous test in echinoids has been studied by several work-

ers. The most important papers in this field are those of Deutler (1926) and Gordon (1926, 1927, and 1929). Deutler's work was based primarily on the species *Echinus esculentus* Linn.; Gordon studied *Psammechinus miliaris* (Gmelin), *Arbacia punctulata* Gray, *Echinocardium cordatum* (Pennant), and *Echinarachnius parma* Lamarck. Reference was also made to other species, and it seems reasonable that the picture developed by these workers can be applied to a study of *Lytechinus* and *Hemicentrotus*.

Immediately following metamorphosis, a young specimen of a regular echinoid species such as *Psammechinus miliaris* is about one millimeter in diameter (with the spines accounting for about half this diameter). Five ocular and five genital plates are present; there is but one plate in each ambulacral column; and there are four plates in each pair of interambulacral columns. Thus, there is a total of ten ambulacral and twenty interambulacral plates at this stage. The plates are calcite and each is a single crystallographic unit, as is indeed the case even before metamorphosis (Lucas, 1953).

The structure of the young sea-urchin, described above, is in sharp contrast with that of the adult form. A specimen of *Hemicentrotus pulcherrimus* having a medial (ambital) diameter of 46 mm. has about 28 interambulacral plates in each column and about 160 ambulacral plates (counting each demi-plate as one) in a column: this makes a total of approximately 1,900 plates in the test, not including the spines, plates of the apical system and peristome, etc.

As the test grows, new plates are added to each column at the end closest to the apical system (in contact with the oculars). As plates are added, existing plates are forced to migrate downward on the test toward the peristome; at no time, however, is the tight mosaic of interlocking plates broken. As a consequence of this mode of growth, a plate which is on the dorsal surface of the test at an early stage will be nearer the peristome at a later stage. A few of the first-formed plates make the complete migration and are actually resorbed at the peristome margin. This process is not thought to continue for long, however; resorption ceases before the test attains an ambital diameter of a few millimeters.

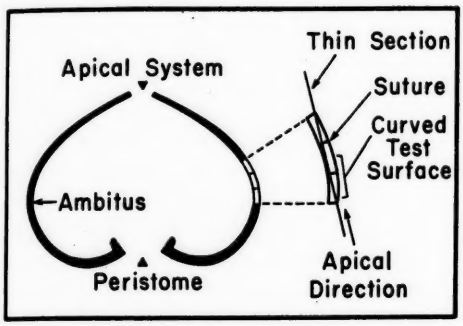
As the test develops, the ambulacral plates generally are differentiated into compound plates, each being made up of several demi-plates. In *L. variegatus* and *H. pulcherrimus*, each compound plate usually consists of four demi-plates, each of which has two pores for tube feet. Other species have a greater or smaller number of these subsidiary plates. *Eucidaris thouarsii* (Valenciennes), for example, undergoes no differentiation in the ambulacra and has only simple columns of crudely hexagonal plates.

The addition of new plates is not the only way in which the test increases in size. Each plate is enlarged by peripheral addition of calcite. Plate accretion leaves a record in a series of concentric "growth rings": the growth rings have been particularly emphasized in the work of Deutler, referred to above. By careful examination of the growth rings, Deutler substantiated the conclusions that Gordon had made on the basis of other lines of evidence. The progressive addition of new plates at the apical system is demonstrated by an increase in the number of growth rings in successive plates from apical system to peristome in a given plate column.

Studies of test development are important to the interpretation of crystallographic data on echinoid calcite for several reasons. In order to compare *c*-axis orientations in plates from different specimens, the relative ages of the plates must be known: it is obvious that coronal plates near the apical systems of two specimens of different sizes are not likely to have been formed at the same stage of development. Also, if the adaptive significance of certain *c*-axis orientations is to be understood, the position on the test of a given plate at various stages of growth must be known. For these and other reasons, frequent reference will be made to test development in the discussion of calcite crystallography that follows.

METHODS

The methods developed by the writer in his earlier work (1959) were employed with little modification in the study of *L. variegatus* and *H. pulcherrimus*. Thin sections were prepared of the plates to be analyzed and a petrographic microscope equipped with a four-axis universal stage was used to make the crystallographic determinations.



TEXT-FIG. 1—Cross-section of echinoid test (*Lytechinus variegatus*) showing orientation of thin section. Test curvature exaggerated for clarity.

Each thin section contained from two to four interambulacral plates and from three to five attached compound plates from the adjacent ambulacral column. The maximum number of plates in any one section was governed by the curvature of the test: portions of the test that were nearly flat could contribute more plates to a thin section than could more sharply curved portions. As few plates as practicable were included in one section to reduce the effect of this curvature. Though an attempt was made to make all thin sections nearly parallel to the test surface, most sections perforce represented planes tangent to curved surfaces. This is illustrated in text-figure 1. If the curvature is ignored and the sections are assumed to be everywhere parallel to the surface, the crystallographic data will be accurate only for the plates near the center of a given section; the observed inclinations of the *c*-axes will be in error near the extremities. This source of error was compensated for by calculating the degree of curvature contained in each section. Large-scale longitudinal profiles of each echinoid test were constructed prior to disarticulation, and the radius of curvature and angle of curvature for each segment to be sectioned were determined graphically. Correction values for each plate were derived from these data and applied to the crystallographic data. The correction was nil for the plates in the center of the segment and gradually increased away from the center.

There were opportunities to check the corrections in cases where parts of one echinoid plate were included in adjacent thin sections. Because no differences in *c*-axis orientation have been observed across single plates, the two fragments present in adjacent sections should, when corrected, yield the same *c*-axis orientation. Furthermore, differences encountered in such pairs should reflect the maximum possible error. Using this relation as a measure of accuracy, the maximum deviation of a corrected value from the true orientation was determined to be about three degrees.

Errors caused by latitudinal test curvature (as opposed to longitudinal, just discussed) within a given segment are also possible, especially in small specimens. As will become apparent below, however, these errors are not critical to the present study and thus were not corrected.

Each thin section was oriented with respect to the center of the apical system of the echinoid as the determinations were made. This was done on the assumption that, on the average, sutures between successive plates in a plate column are perpendicular to a line on the surface of the test connecting the center of the apical system and the midpoint of the suture. Thus, an "apical direction" was determined (under the microscope) for each interambulacral and compound ambulacral plate. When the optical data were plotted in stereographic projection, the zero position on the diagram was taken to be the apical direction and the plane of the projection, the plane of the surface of the plate.

Because the present study had as its primary objective a study of ontogenetic changes in *c*-axis orientation, the sampling of a given specimen was designed to include all the plates in a plate column. The results of the determinations made on such series of plates, when plotted together on a single stereographic diagram, provide a picture of ontogenetic change in orientation pattern from the first formed plates near the peristome to the last formed plates adjacent to the oculo-genital ring. In order that analyses from different specimens could be compared with confidence, analogous plate columns were sampled where possible: ambulacral columns V*b* or I*b* and interambulacral columns 5*a* or 1*a* were used in most instances.

MATERIAL

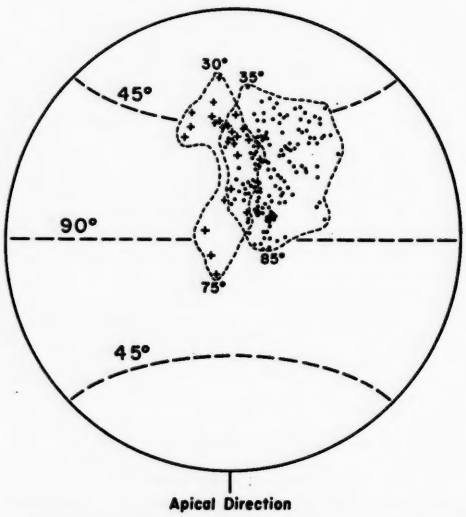
Lytechinus variegatus is primarily a West Indian species but occurs as far north as North Carolina and Bermuda and as far south as Santos on the Brazilian coast (Mortensen, 1943, part 2, p. 444). It is a littoral form though doubtful occurrences at depths of about 300 fathoms have been reported (Agassiz, 1880, p. 78). The specimens used in this study were collected in Harrington Sound, Bermuda. This locality is within the type area for *L. variegatus atlanticus* A. Agassiz.

Hemicentrotus pulcherrimus is restricted to Japan and the northern coast of China (Mortensen, 1943, part 3, p. 254). This species is also a littoral form: it has not been reported from depths greater than 25 fathoms. The specimens used here were collected from three Japanese localities: Takami (near Chocki), Tanabe Bay (near Sirahama), and Naruto (Tokushima Prefecture).

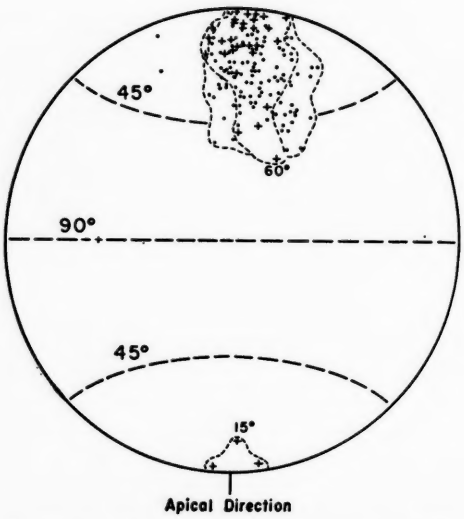
RESULTS

Crystallographic determinations were made on approximately 250 plates from two specimens of *L. variegatus* and 700 plates from five specimens of *H. pulcherrimus*. The data that are plotted in stereographic projection in text-figures 2 and 3 are representative of the results of this study. Columns V*b* and 5*a* from a specimen of *H. pulcherrimus* are represented in text-figure 2. In text-figure 3, an ambulacral plate column (I*b*) and the adjacent interambulacral column (1*a*) from a specimen of *L. variegatus* are shown. In these diagrams, the points are projected from the lower hemisphere. Thus, a point near the top margin of the diagram (side opposite that of the "apical direction") indicates that the *c*-axis of one plate is nearly tangent to the test surface but plunges away from the apical system at a low angle; a point lying near the center of the diagram represents a plate with its *c*-axis nearly perpendicular to the test surface.

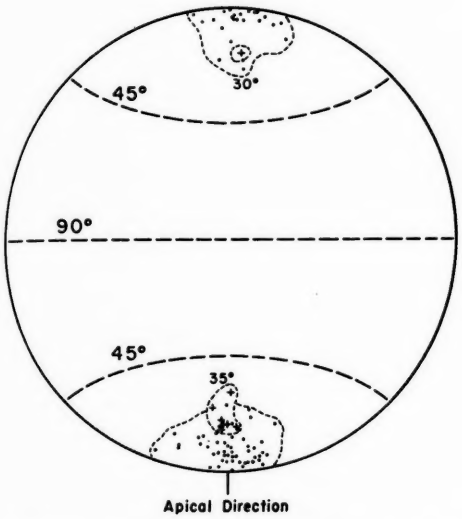
As can be seen in the text-figures, there is an obvious preferred orientation of *c*-axes: in both species, the axes are aligned almost longitudinally. There is some departure from the longitudinal alignment: ambulacral plates plot to the right of a north-south line and interambulacrals plot slightly to the left. This is largely an effect of the lateral test curvature, referred to above, which was



TEXT-FIG. 2—Stereographic projection of *c*-axis orientations in one specimen of *Hemicentrotus pulcherrimus* (amb. diam.: 46 mm.). Crosses: plates from interambulacrum 5*a*; dots: plates from ambulacrum V*b*; numbers indicate angles between test surface and *c*-axes (projected to vertical north-south plane).



TEXT-FIG. 3—Stereographic projection of *c*-axis orientations in one specimen of *Lytechinus variegatus* (amb. diam.: 55 mm.). Crosses: interambulacrum 1*a*; dots: ambulacrum I*b*.

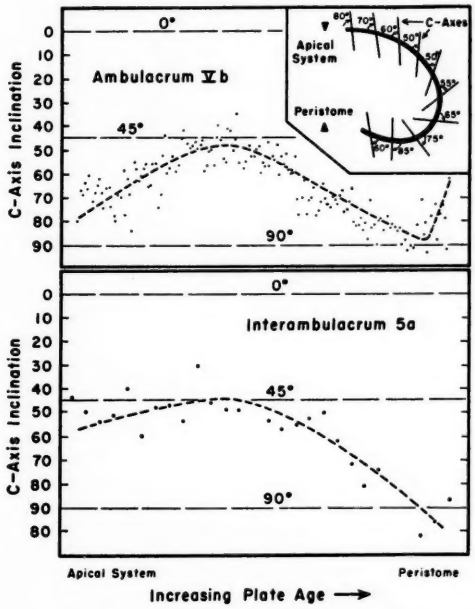


TEXT-FIG. 4—Stereographic projection of *c*-axis orientations in one specimen of *Eucidaris thouarsii*. Crosses: interambulacrum 5*a*; dots: ambulacrum V*b*.

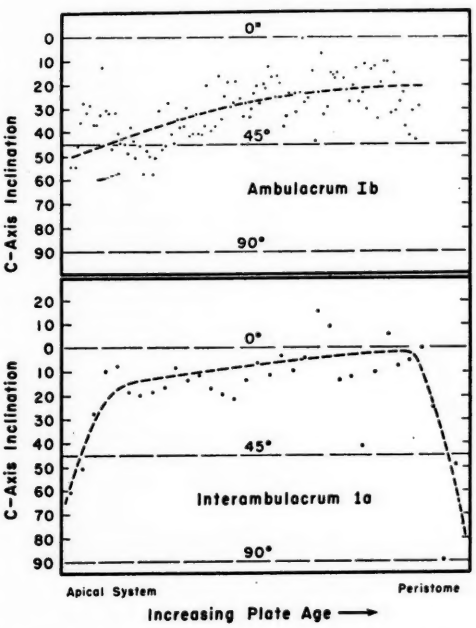
not corrected. If the alternative pairs of plate columns (such as 4*b* and V*a*) had been plotted, the distributions would have been displaced to the left of the north-south line. There is no evidence that the observed displacement cannot be explained in terms of uncorrected test curvature.

The most striking variation shown in the plots is in inclination to the test surface in a longitudinal direction. In *L. variegatus* this ranges from less than zero degrees (tangent) to over 60, and *H. pulcherrimus* from about 30 degrees to over 90 (vertical). Other echinoid species that have been studied crystallographically do not exhibit such variation. For comparison, data from *Eucidaris thouarsii* are reproduced in text-figure 4.

To relate the variation in *c*-axis inclination noted in text-figures 2 and 3 to ontogenetic development, the same data have been replotted in terms only of inclination (text-figs. 5 and 6). In these figures, the angle between the plane of the test surface and the *c*-axis (projected to a vertical plane) is plotted on the ordinate. The units (not shown) on the abscissa correspond to the plates in sequence from apical system to peristome margin. In the case of ambulacral plates, each demi-plate is plotted separately,



TEXT-FIG. 5—*C*-axis inclinations in *Hemicentrotus pulcherrimus* (data from Text-fig. 2). Inset shows same data schematically.



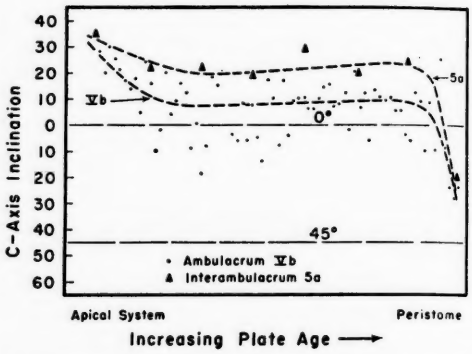
TEXT-FIG. 6—*C*-axis inclinations in *Lytechinus variegatus* (data from Text-fig. 3).

four demi-plates constituting one compound plate in these species. The plates near the peristome (right end of diagram) are the oldest; the plates decrease in age progressively toward the apical system (left of diagram). Again for comparison, similar plots for *Eucidaris thouarsii* are shown in text figure 7.

The data shown in text-figures 5, 6 and 7 are typical of those derived from this study in that they show a tendency for the plates at the extremities of columns to have *c*-axis orientations markedly divergent from the pattern established by the bulk of the plates. For example, the first three and last three plates in the interambulacral column of *L. variegatus* (1*a*) exhibit a higher inclination (25–90 degrees) than most of the other plates in the same column (which are within 20 degrees of the tangent position). Also, the ambulacral plates of *H. pulcherrimus* (V*b*) near the peristome margin appear to depart from the general pattern by having relatively low inclinations. The apparent lack of divergence at the ends of the ambulacral column of *L. variegatus* shown in text-figure 6 is also typical: divergence at the extremities is not universal in the species studied.

The most reasonable explanation for the divergence at the proximal and distal ends of plate columns involves plate rotation. The data suggest that soon after formation (near the apical system), plates are rotated into "normal" position as they migrate away from the oculo-genital ring. In the interambulacral plates of *L. variegatus*, the "normal" position would be that exhibited by the bulk of the plates as shown by text-figure 6: with the *c*-axis nearly tangent to the test surface. In the case of the rotation of the distal plates, it is reasonable that the change in orientation is related to the formation and enlargement of the perignathic girdle. Such rotation is suggested on morphological grounds by Deutler (1926, figs. K-O) in his classic paper on growth in echinoids.

If plate rotation at the ends of columns is disregarded, the data on inclination show definite patterns of variation which are related to growth. The pattern for *L. variegatus* in text-figure 6 may be characterized as showing a gradual decrease in inclination



TEXT-FIG. 7—*C*-axis inclinations in *Eucidaris thouarsii* (data from Text-fig. 4).

with increasing plate age. This is true for interambulacral plates (which show evidence of rotation) as well as ambulacral plates (which do not show evidence of rotation), though both the initial inclination and the rate of decrease in inclination are less in interambulacrals than in ambulacrals. The specimen of *H. pulcherrimus* represented in text-figure 5 exhibits a better defined pattern: along a column from apical system to peristome, inclination in ambulacrals initially decreases from about 75 degrees to about 45 degrees; with increasing age, the trend is reversed by a gradual increase to about 85 degrees in the oldest plates. The same general pattern is observed in the interambulacral plates, though the initial decrease is not pronounced. The data for *Eucidaris thouarsii* show no systematic ontogenetic variation (when divergence at the extremities is disregarded).

Two possible explanations of the changes cited above are apparent: either there is gradual plate rotation throughout the migration of a plate, or plates deposited at various times by the organism have different *c*-axis orientations. It is clear that more data are required to enable one to choose between these alternatives. Therefore, four additional specimens of *H. pulcherrimus* were analyzed. The collecting localities, sizes (ambital diameter), and plate counts for the five specimens are given in Table 1. Ambulacrum V*b* and interambulacrum 5*a* were studied in each, and diagrams similar to those already given were prepared.

In text-figure 8, the *c*-axis inclination data

TABLE 1—DATA FOR FIVE ANALYZED SPECIMENS OF *Hemicentrotus pulcherrimus*

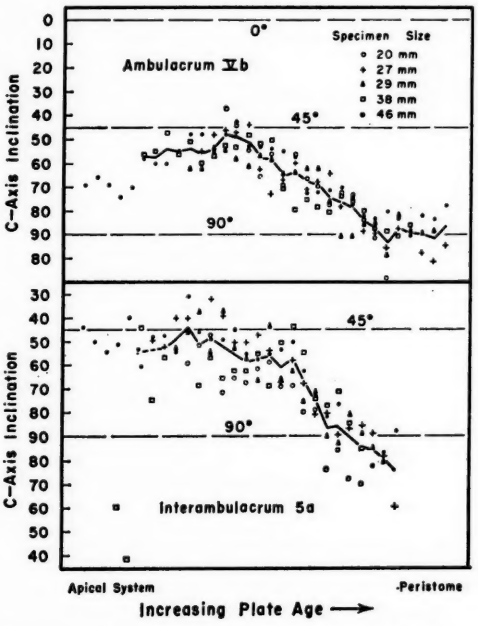
Collecting locality	Amb. Diameter	5*a*	V*b*	2*a*	II*b*	II*a*
Hatake-zima, Tanabe Bay, Japan	20 mm.	16	74			
Hatake-zima, Tanabe Bay, Japan	27 mm.	21	102			
Takami, Japan (U. S. Nat. Mus. #E. 2808)	29 mm.	19	109	5	26	12
Hatake-zima, Tanabe Bay, Japan	38 mm.	20	124			
Naruto, Japan	46 mm.	26	157			
		102	566	5	26	12
			Total: 711 plates analyzed			

for all five specimens are superimposed in one diagram. In constructing this figure, the plates adjacent to the apical system on different specimens were not given the same position on the abscissa because this would be to compare plates formed at differing stages in the growth of the individual. Rather, the distal plates in each specimen were aligned (with allowance for plates lost in sectioning). This scheme is predicated on the assumption that this species is similar to other echinoids in undergoing no significant resorption of plates in the size range from 20 to 46 mm. (ambital diameter). Each point on the curve drawn through the resulting scatter of points is an average of all determinations in a given interval on the abscissa. The curve is omitted in the region at the left end of the diagram because here only the largest specimen (46 mm.) is represented, making the position of the curve less certain. Not every ambulacral plate is shown on the plot: data from successive groups of five demiplates were averaged for simplicity in constructing the figure.

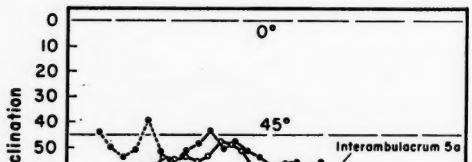
The relatively slight scatter about the curves in text-figure 8 supports the contention that no significant resorption of plates occurs near the peristome margin after an ambital diameter of 20 mm. is attained. If resorption did continue beyond this point, the points at a given interval on the abscissa would refer to plates of differing age and the scatter would be great. Furthermore there does not appear to be significant rotation of plates after they attain the normal position (see above), for this too would increase the scatter. It appears, therefore, that once the plates are formed and begin their migration downward on the test, the *c*-axis orientation is fixed—although there may be some rotation near the peristome margin. More important, however, it is clear that the crystallographic orientation of plates produced near the apical system changes rather regularly throughout ontogeny.

A comparison between ontogenetic trends in ambulacral plates and interambulacral plates is shown in text-figure 9, where the two curves from the previous figure are superposed. Except for the uncertainty in the youngest plates (left end of diagram), the two curves compare favorably.

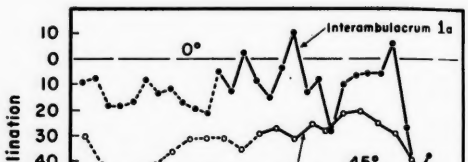
A similar plot for data from two speci-



TEXT-FIG. 8—Summary of data on *c*-axis inclination in ambulacral and interambulacral plates of *Hemicentrotus pulcherrimus*.



TEXT-FIG. 9—Comparison of *c*-axis inclinations in ambulacral and interambulacral plates of *Hemicentrotus pulcherrimus* (data from Text-fig. 8).



TEXT-FIG. 10—Comparison of *c*-axis inclinations in ambulacral and interambulacral plates of *Lytechinus variegatus*.

mens of *L. variegatus* (one of which was used for text-fig. 3) is shown in text-figure 10. Because the measurements of complete plate columns in this species are limited to two specimens from a single locality, the results cannot be considered conclusive. The data are presented, however, to emphasize the fact that the picture described for *H. pulcherrimus* is by no means universal: the curves for the two species would barely overlap if superposed. Furthermore, text-figure 10 suggests that in one species, at least, the ambulacral plates have *c*-axis orientations that are consistently different from those of interambulacral plates. This was also found to be the case in species that do not show ontogenetic variation in calcite orientation (Raup, 1959.)

INTERPRETATION

The results of this study indicate that some species of echinoids have the genetic ability to alter the crystallographic orientation of coronal plates as they are formed at the apical system. This fact may provide a basis for understanding the evolution of echinoid groups with markedly different relations between morphology and *c*-axis orientation.

To review earlier work (Raup, 1959), all species of the family Cidaridae (fossil and Recent) that have been studied crystallographically have *c*-axes that are nearly tangent to the test surface; the pseudodiadematids, presumed to have evolved from the cidarids, have axes perpendicular to the test surface; the families Toxopneustidae (excepting *Lytechinus variegatus*) and Temnopleuridae (both derived from the Pseudodiadematidae) have tangential *c*-axes. This evolutionary pattern could have been brought about by shifts in growth rates in species exhibiting ontogenetic variation in *c*-axis orientation. Suppose that in a hypothetical species, similar to *H. pulcherrimus*, the first formed plates had perpendicular *c*-axes and the last formed plates had tangential *c*-axes. If the perpendicular orientation were environmentally advantageous, developmental rates might be altered so that plates were laid down with nearly perpendicular axes throughout most or all of the ontogeny of the individual. This would represent the process of neoteny, described by de Beer (1958, p. 27) and others. The reverse case is also possible provided that tangential *c*-axes have the selective advantage. Though no exact counterpart of this hypothetical species has been found, both *H. pulcherrimus* and *L. variegatus* differ from it only quantitatively.

If the evolution of one preferred orientation from another is to come about in the manner just outlined, what selective advantage could a given orientation of *c*-axes have? A possible answer to this question is to be found in the normal reactions to light among living echinoids. It is well known that some species are light negative (avoiding light) and some are not. Light negative echinoids in the littoral zone characteristi-

cally hide from bright sunlight (in crevices or under stones) or cover their tests with debris (bits of shell, pebbles, plant material, and the like). The covering habit has attracted much study: reviews are to be found in the works of Hyman (1955, p. 551), Harvey (1956, p. 43–44), Mortensen (1943, part 3, p. 135), and Millott (1956, 1957). There is little doubt among these authorities that the covering reaction is for the purpose of shielding the test from light, not for camouflage or some other purpose.

The echinoid's sensitivity to light does not seem to be limited to the external surface of the test. Millott (1954) has shown, through laboratory experiments with living echinoids, that the nervous tissue lying just under the calcite test is extremely sensitive to light: normal light reactions may be stimulated when only this subskeletal tissue is exposed to light. Millott's studies on light negative forms further suggest that sunlight normally passes through the calcite test of the living echinoid. It would appear, therefore, that a test which transmitted little light would be of advantage to light negative species and perhaps would even eliminate the necessity of covering the exterior of the test with debris.

A survey of pertinent literature indicates that littoral species with tangential *c*-axes are more apt to be light negative than those with perpendicular *c*-axes. A comprehensive study of this relation from the literature is hampered by the fact that reference is rarely made to forms which do not exhibit the characteristics of light negativity. *Diadema antillarum* Philippi provides an exception in that its light sensitivity has been studied by Millott. Millott (1954, p. 189) summarizes his observations on this species as follows: " . . . [a] large number exist in a few inches of water, fully exposed to the tropical sunlight, the effect of which they appear to be able to tolerate indefinitely." *Diadema antillarum* has perpendicular *c*-axes (Raup, 1959).

A similar case is that of *Strongylocentrotus dröbachiensis* (Müller). This species shows none of the characteristics of the light negative form (Mortensen, 1943, part 3, p. 209) though it is closely related, both taxonomically and ecologically, to species which have the covering habit: *Paracentrotus lividus* (Lamarck), for example. *Strongylocentrotus dröbachiensis* has perpendicular *c*-axes and *Paracentrotus lividus* has tangential *c*-axes (Raup, *op. cit.*). Other species that are light negative and that have tangential *c*-axes are *Psammechinus microtuberculatus* (Blainville) *Ps. miliaris* (Gmelin), *Tripneustes gratilla* (Linn.) *Pseudoboletia indiana* (Michelin), *Parechinus angulosus* (Leske), and *Arabacia lixula* (Linn.). *Lytechinus variegatus* and *Hemicentrotus pulcherrimus* are both light negative and, as we have seen, have *c*-axis orientations on the aboral surface that approach the tangential. A puzzling exception to the above generalizations is *Evechinus chloroticus* (Valenciennes), a species that has perpendicular *c*-axes but which is, according to Mortensen, light negative.

To explain the apparent correlation between crystallography and light sensitivity, reference must be made to the internal structure of the echinoid plate. As has often been noted, the plate has a spongelike appearance in thin section, the open spaces in a calcite network being filled with organic tissue. Transmission of light through such a structure will depend in large part on the differences in index of refraction between the network and the material filling it. In the present case, the mean refractive index of the organic tissue is about 1.58 (as determined with living material of *Lytechinus variegatus*); the index of echinoid calcite varies between 1.48 and 1.65 (Merker, 1919, p. 59–60), depending on crystallographic orientation. If the indices of the two substances are nearly identical, light will readily pass through. But if the two differ markedly, internal reflection and refraction will scatter much or all of the light. Because the mineral calcite is uniaxial negative, the difference between the indices of the calcite and organic tissue is at a maximum where the *c*-axes are perpendicular to the incident surface and decreases as the inclination of the axes is lowered.

The effectiveness of internal scattering in reducing light transmission through echinoid plates has been tested in the laboratory by immersing whole plates in liquids of varying refractive index. Strongly convergent light was used to simulate natural conditions, where perpendicular incidence of light on the test surface cannot be assumed. The

differences in light transmission produced by altering the index of the liquid are striking, though whether the differences would be significant under natural light conditions is not known. It is suggested, however, that echinoid species which do not appear to be light negative are protected from sunlight by the perpendicular *c*-axis orientation. Orientation would be most critical, of course, on the fully exposed dorsal surface of the echinoid. Those species which are obviously light negative generally have tangential *c*-axes and are protected from sunlight by other means, such as covering with debris.

It is obvious that more information is needed before the adaptive significance of echinoid *c*-axis orientations can be explained confidently in terms of light. A more comprehensive study should be made of echinoid behavior and echinoid crystallography to build up empirical evidence on correlations between these two factors. Of particular interest in this regard would be further study of *H. pulcherrimus*. Because coronal plates near the peristome in this species have perpendicular axes, it might be found that juvenile forms (which would have *only* perpendicular *c*-axes) do not appear light negative. The young individuals would, by virtue of their crystallography, be relatively insensitive to light in the period of growth before the ability to cover the test with debris developed. On the other hand, the extremely thin test of the immature form might make necessary the added protection against sunlight afforded by perpendicular *c*-axes, even though other means of protection were available.

If further study supports the conclusions indicated by the evidence presented in this paper, the relations between crystallography and ecology will be important in understanding echinoid evolution and fossil echinoid environments.

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JOURNAL OF PALEONTOLOGY, V. 34, NO. 5, P. 1051–1053, 1 TEXT-FIG., SEPTEMBER, 1960

PALEONTOLOGICAL NOTE

THE PHYLOGENETIC CLASSIFICATION OF THE MADREPORARIAN CORALS

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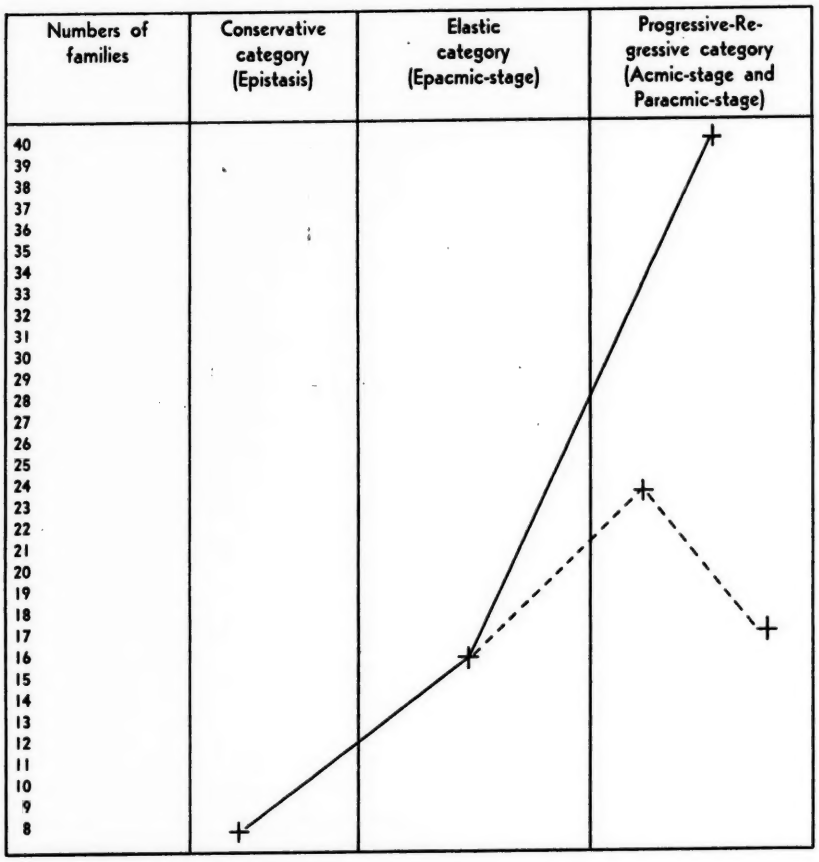
As a result of my "System of the life phenomena" (1953), I am proposing a new phylogenetic classification of the Madreporarian corals.

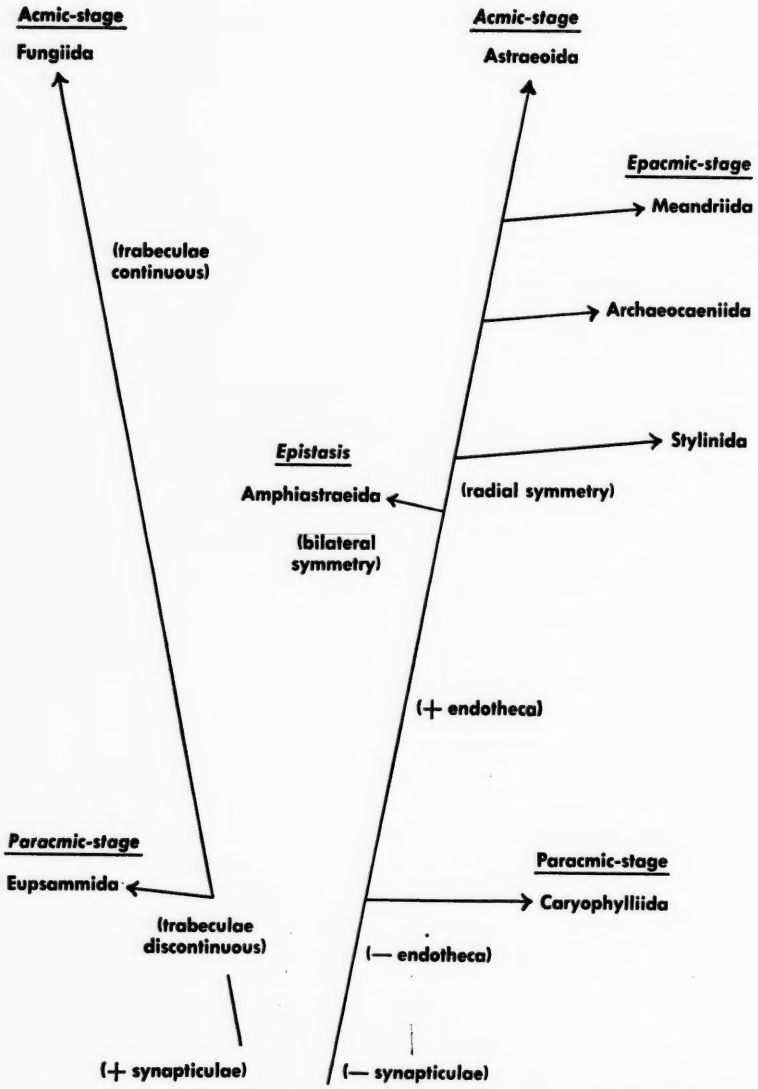
The 8 suborders of the recent and fossil Madreporarian corals proposed by Alloiteau in Piveteau, (1952) with their included families are as follows:

Suborder 1	Archaeocaeniida.....	6 families
Suborder 2	Stylinida.....	4 families
Suborder 3	Astraeoida.....	16 families
Suborder 4	Meandriida.....	5 families
Suborder 5	Amphiastraeida.....	2 families
Suborder 6	Caryophylliida.....	6 families
Suborder 7	Fungiida.....	24 families
Suborder 8	Eupsammida.....	2 families

In the acmic-stage are the fungiids and the astraeoids with many families. They form a highly differentiated phylogenetic group. These suborders show most clearly the progression of the phylogeny of the

TABLE 1—STATISTICAL GRAPH OF CORAL CATEGORIES





TEXT-FIG. *1*—Phylogenic classification of the Madreporarian corals.

madreporarian corals. Regressive suborders are the eupsammids and the caryophylliids with few families. The eupsammids have discontinuous trabeculae and the Caryophylliida are without endotheca.

The elastic (epacmic) group composed of the suborders Meandriida, Archaeocaeniida, and Stylinida have various phylogenetic characters.

The conservative (paracmic) group contains the suborder Amphiastraeida with bilateral symmetry of the septa and contains only 2 families. The conservative group (epistasis) includes the primitive bilateral characters; the elastic group includes the forms with accommodative characters. This represents the middle value between the two extreme categories (conservative and pro-

TABLE 2—NATURAL CLASSIFICATION OF MADREPORARIAN CORALS

The groups of my "System"	Natural sequence of the suborders	After Kolosváry (1953)	After Alloiteau (1952)
I. Conservative	1	Bilaterality: Amphiastraeida	1. Archaeocaeniida
II. Elastic	2	Few septa: Stylinida	2. Stylinida
	3	Many septa: Archaeocaeniida	3. Astraeoida
	4	Meandriida	4. Meandriida
III. Progressive and Regressive	5	Dominant: Astraeoida	5. Amphiastraeida
	6	Recessive: Caryophylliida	6. Caryophylliida
	7	Dominant: Fungiida	7. Fungiida
	8	Recessive: Eupsammida	8. Eupsammida

gressive). The progressive-regressive category includes the mobile groups with their many families (dominancy).

The statistical graph (Table 1) illustrates this categorization of my "System of the life phenomena."

The table (Table 2) illustrates my natural (genetic) series of the classification of the recent and fossil Madreporarian corals based on the categorization of my "system" (1953) compared with that of Alloiteau (1952).

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NOMENCLATURAL NOTES

WELLSOTROCHUS, A NEW NAME FOR *WELLSIA* SQUIRES, 1958

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The generic name *Wellsia* (Squires, 1958, p. 57) proposed for a Cretaceous turbinoliid coral is preoccupied and must be replaced. The prior usage of this name is by Imlay (1957, p. 275) in reference to an early Cretaceous ammonoid from the west coast of the United States. For *Wellsia* Squires, 1958, preoccupied , I propose *Wellsotrochus*, n. name, with the types species *Wellsotrochus cyathiformis* (Squires), 1958. *Wellsotrochus* is proposed to honor Dr. John W. Wells, while *Wellsia* Imlay honors Dr. Francis G. Wells. I am grateful to Mr. Jack Grant-Mackie, Auckland University, for calling my attention to this homonymy.

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SOKOLOPHOCOLEUS, NEW NAME FOR THE MACHAERIDIAN GENUS, *LOPHOCOLEUS* RUEDEMANN

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Ruedemann, 1901, p. 578, pl. 2, figs. 16–25, gave the name *Pollicipes siluricus* to isolated Machaeridian plates from the Ordovician, Snake Hill shale, of New York State. The species was assigned to the genus *Pollicipes* Leach in accordance with the notion of the cirriped affinity of the Machaeridia. With the admittance of the Machaeridia into the Echinodermata, Ruedemann, 1942, p. 40, erected the genus *Lophocoleus*, type species, *P. siluricus*.

Lophocoleus Ruedemann, 1942, is a homonym of *Lophocoleus* Butler, 1886, p. 416, a genus of Lepidoptera. I propose the name *Sokolophocoleus* (*sokos*, stout; *lophos*, crest; *coleus*, sheath) to replace *Lophocoleus* Ruedemann. The type species remains *P. siluricus*.

These names have been investigated in the *Zoölogical Record* and S. A. Neave, *Nomenclator Zoölogicus*. I wish to thank R. S. Bassler, R. F. Hecker, G. Regnéll and G. Ubaghs for their counsel.

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REC'D. JUNE 12, 1960

CHANGE OF NAME FOR A CRETACEOUS CHIMAEROID

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University of California Museum of Paleontology

Characteristic fossil chimaeroid egg-cases ranging in age from Jurassic to Oligocene were described as six new species and referred to a new form-genus *Chimaerotheca* by Brown (1946). Among these, the name *C. wyomingana* was given (*ibid.*, p. 263) to a specimen from the Upper Cretaceous Mesaverde formation near Laramie, Wyoming. This specimen was previously named *?Elasmodus gilli* by Hay (1930, p. 615) and now becomes *Chimaerotheca gilli* (Hay) Brown.

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SOCIETY RECORDS AND ACTIVITIES

In accordance with Article 3, Chapter 1, of the By-Laws of the Paleontological Society, the names of new members approved by the Council are as follows:

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PACIFIC COAST SECTION

The following officers were elected at the May 6 meeting of the Pacific Coast Section of the Paleontological Society:

Chairman —H. J. Bissell
Vice-Chairman—C. A. Nelson
Secretary —D. L. Jones
Councilor —O. L. Bandy

OBITUARY

Paleontologists everywhere will be saddened by the death of J. Brookes Knight at his Florida home on March 21, after a long illness. At the request of the family, tribute to the memory of Brookes by his friends at the time of the funeral took the form of contributions to the Endowment Fund of the Paleontological Society. Other friends and colleagues may wish to join in this fitting tribute to a distinguished paleontologist and former President of the Society. The progress of paleontology and the affairs of the Society were always matters of deep concern to Brookes Knight.

Contributions to the Endowment Fund of the Paleontological Society in tribute to J. Brookes Knight should be sent to Dr. Claude C. Albritton, Jr., Treasurer of the Paleontological Society, Department of Geology, Southern Methodist University, Dallas 22, Texas.

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